



**PHD**

**Ecological and life-history basis of wetland bird conservation: Phylogenetic and spatial analyses**

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# **Ecological and life-history basis of wetland bird conservation: phylogenetic and spatial analyses**

Peter Richard Long

A thesis submitted for the degree of Doctor of Philosophy

University of Bath

Department of Biology and Biochemistry

July 2008

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## Summary

Wetlands are globally distributed, diverse and some of the most productive ecosystems on the planet. Many wetlands, however, are highly threatened by human activities. Since wetlands are so important for biodiversity and for ecosystem services that they provide to people, it is essential that they are managed responsibly. The objective of my PhD was to build on recent advances in phylogenetic and spatial analyses to inform conservation of wetland biodiversity. First, many wetland bird species, especially in the tropics, are poorly studied and we often lack information about their distribution and abundance. Using a habitat suitability model I demonstrate that it is possible to combine spatially-referenced field observations with satellite imagery to estimate the population size of a threatened tropical shorebird, the Madagascar plover *Charadrius thoracicus*. Second, I used phylogenetic comparative analysis to explore factors associated with population declines in wildfowl and found that ecological factors (population and range size) and human effects (agriculture and multiple threat processes) both contribute to population declines in wildfowl. Third, I then modeled population trends in 23 taxonomic groups of wetland birds and tested whether the main processes driving population declines are consistent between groups, concluding that species conservation prioritisation must take account of the idiosyncratic ways in which different groups may become threatened. Fourth, I turned to spatial techniques in order to investigate the characteristics of wetlands in a landscape context which account for patterns of diversity in wetland bird communities in Europe. Results of this latter work suggested that large wetlands at low elevations in southern Europe which are well connected to other wetlands are associated with the most diverse communities. It is also possible for rich and diverse wetland bird communities to coexist with a relatively high density of people in Europe. Fifth, at global scale, although the extent of wetlands has been inventoried, we have no consistent measure of global wetland changes. I addressed this issue by performing a change analysis on an 18 year time series of satellite data to determine the global trajectory of wetland change for the first time, and map net changes in wetland area between 1982 and 2000. Globally 7.51% of wetlands were lost in this period. In conclusion, my thesis demonstrates the need for integrating ecosystem, community and species-level approaches. The results of these studies will impact on wetland bird conservation globally, and specifically, in Madagascar.

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## **Chapter 1.** Introduction

P.R. Long

## **Introduction**

Wetlands are highly productive, diverse globally distributed ecosystems characterised by the presence of a water table between 0.3m below the substrate and 2m above (Mitsch & Gotteschalk 2008). Wetlands are spatially heterogeneous, dynamic ecosystems which often occur across ecotones between terrestrial and aquatic systems. They include lakes, rivers, marshes, bogs, fens, mangroves, saltmarshes and flooded forests. These systems support considerable biodiversity, including both obligate and facultative wetland organisms, and are especially important for flowering plants, molluscs, insects, freshwater fish, amphibians and birds (Millennium Ecosystem Assessment 2005; Dudgeon et al. 2006).

Wetland birds have been particularly well studied and monitored. Depending on the stringency of the measurement criteria, between 5% and 10% of all bird species are dependent on wetland ecosystems for some part of their life cycle. BirdLife International (2000), estimate that there are 1000 wetland bird species, whereas Dehorter and Guillemain (2008) argue that only 566 bird species imperatively need freshwater wetlands to satisfy at least one of their life-history stages. Monitoring data from wetland bird populations has been systematically collected globally since 1994 (Rose & Scott 1994) and a comprehensive inventory is now published at approximately three year intervals (Wetlands International 2006). Wetland birds are also recognised to be particularly good indicator species for the health of wetlands since they are relatively large organisms and often at a relatively high trophic level (Furness & Greenwood 1993).

Liquid freshwater in wetlands, soils and plants makes up only 0.77% of all the water on earth (Shiklomanov 1993). It is a scarce and exceptionally valuable resource since it is unsubstitutable in many of its uses including as a habitat, as drinking water and for growing crops.

Unfortunately, wetlands across the world are threatened by a number of processes including drainage and conversion to agricultural land, over-harvesting of natural resources, changes to the hydrological regime, pollution and invasive species (Moser et al. 1996). Human pressures on wetlands, including water extraction, land use change and exploitation of biological resources have increased substantially over the last 50 years as a result of human population growth and increasing economic activity to levels which may be unsustainable in the long-term. For example, global water abstraction from wetlands alone has tripled in this period to approximately 4430km<sup>3</sup> per year (Postel et al. 2006).

In the planning of the sustainable use of wetlands, it is important to take account of the ecosystem services that they provide. These include water supplies essential to human health (McMichael 2000), goods such as fish and crustaceans, regulatory services such as flood defence and pollution dilution, and the recreational and cultural values of wetlands.

A great diversity of global conservation prioritisation exercises have been undertaken to inform the allocation of scarce conservation resources such that they have maximum conservation impact in ensuring the persistence of biodiversity. For a review, see Brooks et al. (2006). Estimates of ecosystem services are now being incorporated into some conservation planning, a positive development, since new and diverse stakeholders can be brought into a debate about conservation, by appealing to economic values in addition to intrinsic values of biodiversity (Armsworth et al. 2007).

Conservation scientists have recognised that wetlands are complex, diverse, valuable and threatened systems and that conservation planners, decision-makers and practitioners need adequate data about wetland ecosystems and processes to make informed choices. Nonetheless, there are many potential approaches to studying wetlands and contributing to wetland conservation. These span biodiversity assessments, monitoring programmes, wetland inventories, remote sensing of wetlands, spatially explicit ecological modelling, investigations of biogeochemical cycling, autecological studies of key species, comparative methods and ecological economics and social science.

Considerable progress has recently been made in developing efficient methods for applying ecological data to conservation policy by allocating scarce conservation resources across landscapes, and scheduling investments (Margules & Pressey 2000; Sarkar et al. 2006; Margules & Sarkar 2007), planning for ecosystem services and biodiversity (Chan et al. 2006) and conservation investment scheduling (Murdoch et al. 2007) to wetland ecosystems (Thieme et al. 2007; Moilanen et al. 2008). However, the utility of outputs produced by these tools critically depends on the availability of high quality biodiversity and landcover and other ancillary data, emphasising the continued need for fundamental studies of wetland species and ecosystems in addition to sound conservation synthesis and planning.



Pluralism, the affirmation and acceptance of a diversity of approaches, is an important social and political concept but is perhaps even more important in a crisis discipline such as conservation. When agency to undertake research, set conservation priorities and take action is distributed among a diverse global community of scientists, non-governmental organisations, local people and national governments, there will inevitably be many different approaches to understanding the status of the natural environment.

In this thesis I explore several complementary approaches to understanding the status of wetland birds and wetland environments across different levels of organisation (individuals, species, communities and ecosystems), spatial scales (local, regional, continental and global) and temporal scales (Table 1). The overall aim is to produce methods and data which can inform wetland conservation.

**Table 1** – Chapter summaries

Ch	Type	Ecol scale	Ecol scope	Geog scale	Geog extent	Temp scale	Temp scope	Explanatory variables (significant in bold)
2	Predictive	Individuals	633 Madagascar plover	30m raster	242445 km <sup>2</sup> of Madagascar	2 years	2003-2005	<b>Brightness, Moistness, Greenness, Elevation, Settlements, Coast</b>
3	Explanatory	Populations	347 wildfowl populations of 130 species	N/A	Global	8 years	1994-2002	<b>Population size, Range, Migration, Habitat, Trophic level, Latitude, Mass, Fecundity, Testes, Threats, Human population, Water consumption, Agriculture</b>
4	Explanatory	Species	600 wetland bird species in 23 groups	N/A	Global	12 years	1994-2006	<b>Mass, Population size, Latitude, Human population, Mass*Human population</b>
5	Explanatory	Communities	Species Richness and diversity across 2012 IBAs	Vector presented as 1 degree grid	Europe	1 year	1996-1997	<b>Area, Habitat diversity, Elevation, Latitude, Nearest neighbour, Human population</b>
6	Descriptive	Ecosystem	Wetlands	8km raster	Global	18 years	1982-2000	N/A

Effective planning of protected area networks and other conservation measures requires techniques for leveraging limited data concerning poorly-known species to produce accurate estimates of the abundance and distribution of these species in large landscapes. To address the latter problem, I used a geographic information system to determine whether readily available spatial data can successfully describe the distribution of endangered waterbirds. I chose to use data from Madagascar plover *Charadrius thoracicus*, because little is known about its distribution and since the road system in Madagascar has precluded comprehensive surveys, to produce a predictive spatial model which allowed population size to be estimated using additional data on the density of Madagascar plover in suitable sites. (Chapter 2).

In order to understand the basis for the variation in threat between species. I considered just one order of wetland birds, wildfowl, and used phylogenetic comparative analyses to identify the ecological, life-history and anthropogenic factors that make some duck, goose and swan species more threatened than others. I asked how intrinsic aspects of a species' biology and extrinsic human influences within a species' range contribute to the population trend of wildfowl and we assess the relative importance of population size and range, ecological traits, life-history traits, sexual selection and anthropogenic threat processes in the global range of each species. In addition, I test whether intrinsic biological traits make wildfowl species more susceptible to extrinsic threats. (Chapter 3).

Species prioritisation efforts depend on accurate assessments of threats to species and the processes driving these threats. To better understand the mechanisms threatening wetland birds, I modelled the factors associated with declining population trends among all species of wetland birds and then compared 23 taxonomic groups of wetland birds with my overall model to identify groups of birds which are threatened in idiosyncratic ways. I also explore why species prioritisation for conservation may need to take special account of taxonomy (Chapter 4).

In order to better understand wetland bird communities in a landscape context at continental scale, I explored the patterns of species richness and diversity of birds which are ecologically dependent on wetlands in terms of environmental characteristics of wetlands and measures of human impact using 2012 European Important Bird Areas (IBAs) which contain wetlands. I tested the effects of wetland area, habitat diversity, elevation, latitude, isolation from nearest neighbouring wetland and human population density in a buffer surrounding the wetland. My

results suggest the most important properties of wetland habitats which can promote wetland rich and diverse wetland bird communities at large spatial scales (Chapter 5).

Although global wetland inventories have been produced, and estimates of wetland change in some regions of the world exist, there is a need for a globally consistent estimate of wetland change over a relatively long period in the recent past in order to understand which wetland systems are most threatened by land use change. This is a tall order, and no study has appeared to respond to this demand. To address it, I performed a change analysis of multi-temporal Advanced Very High Resolution Radiometer (AVHRR) satellite images to measure proportional wetland area at 8km resolution with a linear spectral mixture model in each month in an 18 year period from 1982 to 2000. By then calculating the minimum and maximum wetland extent in every 8km pixel in each of these years, we distinguished seasonal variation from long-term trends in wetland area over this period in order to map global patterns of net wetland change in space and trajectories of loss through time (Chapter 6).

Taken together, these studies consistently suggest that wetlands face a very uncertain future. Although some species and groups are more resilient than others and some parts of the world have experienced relatively low rates of wetland loss, there are many places where wetlands are highly threatened. Madagascar, my focus of detailed study, is certainly not unique in this respect. For example, triangulating the findings that Asia has disproportionately many threatened wetland bird species (chapter 3), and the greatest rates of wetland loss in the recent past (chapter 6), indicates that Asian wetlands should be a high global priority for conservation.

Clearly, no single set of actions, such as protected areas, intensive species management or incentives for responsible use of wetlands will be appropriate to ensure the persistence of wetland ecosystems, the species that depend on them and the services they supply. Similarly, the outputs of a diverse research community incorporating many of ways of looking at the environment at different levels of organisation and spatial scales and through different paradigms is needed to help conservation practitioners and key decision makers implement effective conservation action. I believe the future of wetland conservation will depend on sound science, greater dialogue between scientists and conservationists on the ground and political will to recognise the value of wetland and ensure adequate resources for wetland conservation.

## References

- Abell, R. (2002) Conservation biology for the biodiversity crisis: a freshwater follow-up. *Conservation Biology* 16: 1435-1437
- Armsworth, P.R., Chan, K.M.A., Daily, G.C., Ehrlich, P.R., Kremen, C., Ricketts, T.H., & Sanjayan, M.A. (2007) Ecosystem-service science and the way forward for conservation. *Conservation Biology* 21: 1383
- BirdLife International (2000) *Threatened birds of the world*. Barcelona and Cambridge, UK. Lynx Edicions and BirdLife International
- Brooks, T.M., Mittermeier, R.A., da Fonseca, G.A.B., Gerlach, J., Hoffmann, M., Lamoreux, J.F., Mittermeier, C.G., Pilgrim, J.D. & Rodrigues, A.S.L. (2006) Global Biodiversity conservation priorities. *Science* 313: 58-61
- Chan, K.M.A., Shaw, M.R., Cameron, D.R., Underwood, E.C., & Daily, G.C. (2006) Conservation planning for ecosystem services. *PLoS Biology* 4: 2138-2152
- Daily, G.C. (ed.) (1997) *Nature's services: societal dependence on natural ecosystems*. Washington DC, Island Press
- Dehorter, O., & Guillemain, M. (2008) Global diversity of freshwater birds (Aves). *Hydrobiologia* 565: 619-626
- Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.H., Soto, D., Stiassny, M.L.J., & Sullivan, C.A. (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* 81: 163-182

Furness, R.W. & Greenwood, J.J.D. (Eds) (1993). *Birds as monitors of environmental change*. London:Chapman & Hall.

Holmlund, C.M., & Hammer, M. (1999) Ecosystem services generated by fish populations. *Ecological Economics* 29: 253-268

Margules, C.R. & Pressey, R.L. (2000) Systematic conservation planning. *Nature* 405:243-253

Margules, C.R., & Sarkar, S. (2007) *Systematic conservation planning*. Cambridge University Press

McMichael, T. (2001) *Human frontiers, environments and disease: past patterns, uncertain futures*. Cambridge University Press

Mitsch, W.J., & Gosselink, J.G. (2008) *Wetlands, 4th edition*. Wiley.

Moilanen, A., Leathwick, J., & Elith, J. (2008) A method for spatial freshwater conservation prioritisation. *Freshwater Biology* 53: 577-592

Moser, M., Prentice, C. & Frazier S. (1996). A global overview of wetlands loss and degradation. In Technical session B of the RAMSAR Conference of Parties (COP): 21–31. New York & Brisbane: UNFCCC.

Reinthal, P.N., Riseng, K.J., & Sparks, J.S. (2003) Water management issues in Madagascar: biodiversity, conservation and deforestation. In, Crisman, T.L., Chapman, L.J., Chapman, C.A., Kaufman, L.S. (eds) *Conservation, ecology and management of African fresh waters*. University Press of Florida. pp124-142

Sarkar, S, Pressey, R.L., Faith, D.P., Margules, C.R., Fuller, T., Stoms, D.M., Moffett, A., Wilson, K.A., Williams, K.J., Williams, P.H., & Andelman, S. (2006) Biodiversity conservation

planning tools: present status & challenges for the future. *Annual Review of Environment & Resources* 31:123-159.

Shiklomanov, I.A. (1993) World freshwater resources. In, Gleick, P.H. (ed.) *Water in crisis: a guide to the world's freshwater resources*. pp 13-24. Oxford University Press, New York.

Thieme, M., Lehner, B., Abell, R., Hamilton, S.K., Kelndorfer, J., Powell, G., & Riveros, J.C. (2007) Freshwater conservation planning in data-poor areas: an example from a remote Amazonian basin (Madre de Dios river, Peru and Bolivia). *Biological Conservation* 135: 484-501

Millenium Ecosystem Assessment (2005) *Ecosystems and human well-being: wetlands and water synthesis*. World Resources Institute, Washington D.C.

Murdoch, W., Polasky, S., Wilson, K.A., Possingham, H.P., Kareiva, P., & Shaw, R. (2007) Maximizing return on investment in conservation. *Biological Conservation* 139: 375-388

Postel, S.L. (2003) Securing water for people, crops and ecosystems: new mindset and new priorities. *Natural Resources Forum* 27: 89-98

Rose, P.M., & Scott, D.A. (1994) *Waterfowl population estimates*. International Waterbirds and Wetlands Research Bureau, Slimbridge, Gloucestershire

Wetlands International (2006) *Waterbird population estimates*. 4<sup>th</sup> edition. Wageningen, The Netherlands, Wetlands International

**Chapter 2.** Estimating population size of an endangered shorebird, the Madagascar plover, using a habitat suitability model

Peter R. Long, Sama Zefania, Richard ffrench-Constant and Tamás Székely (2008)

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**P.R. Long:** spatial analysis, manuscript writing (70%)

**S. Zefania:** field data collection, editing of the manuscript (20%)

**R. ffrench-Constant:** suggestions to improve the study (5%)

**T. Székely:** general editing of the manuscript, suggestions to improve the study (5%)

# Estimating the population size of an endangered shorebird, the Madagascar plover, using a habitat suitability model

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## Keywords

wader; species distribution model; geographic information system; remote sensing; ecological niche factor analysis.

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## Abstract

The Madagascar plover *Charadrius thoracicus* is a shorebird endemic to western Madagascar, currently classified as globally vulnerable. It is restricted to specialized wetland habitats that are increasingly threatened by humans. To inform future conservation measures for this poorly known species, we develop a predictive habitat suitability map and use this map to estimate the size of the Madagascar plover population. We integrate spatially referenced presence-only observations of Madagascar plovers with Landsat data, elevation data and measures of distance to settlements and the coast to produce a habitat suitability model using ecological niche factor analysis. Validation of this model using a receiver operating characteristic plot suggests that it is at least 84% accurate in predicting suitable sites. We then use our estimate of total area of suitable habitat above a critical suitability threshold and data on Madagascar plover density in suitable sites to estimate the total population size to derive a total population estimate of  $3100 \pm 396$  standard error individuals. Finally, we explore the conservation applications of our model.

## Introduction

The Madagascar plover *Charadrius thoracicus* is a threatened endemic shorebird currently classified as vulnerable [VU C2a(i); D1; BirdLife, 2004]. This species occurs mainly along the west coast of Madagascar between Bombetoka bay in the North and Taolagnaro in the South. This plover uses the edge of lagoons, coastal grassland and mud, and is dependent upon saltmarsh for breeding. The global population size was estimated to be 750–6000 individuals (Birdlife, 2004).

Wetlands are among the most diverse ecosystems in Madagascar and they provide vital ecosystem services to people. Unfortunately, they are increasingly threatened by siltation from deforestation in their catchments, conversion of wetlands to rice paddies and by the expansion of fisheries and shrimp farming (Durbin, Bernard & Fenn, 2003).

In order to better understand species–habitat relationships and distributions, a number of techniques for predictive modelling based on species observations and environmental data have been developed (for reviews, see Guisan & Zimmermann, 2000; Gottschalk, Huettmann & Ehlers, 2005). However, there have been few studies of large-scale habitat suitability for shorebirds (sandpipers, plovers and allies; Avery & Haines-Young, 1990; Gratto-Trevor, 1996), although 16 species are globally threatened (BirdLife, 2004) and 56% of shorebird populations are declining (Wetlands International, 2006).

Predictive habitat models based on the requirements of a species over large geographical areas have a wide range of uses in landscape ecology, conservation biology and wildlife management (Akçakaya & Atwood, 1997; Dettmers & Bart, 1999). Predicted distributions based on habitat associations can provide a higher level of resolution than the fragmentary distribution data that exist for most species in Madagascar (Scott *et al.*, 1993). Such models may also inform further ecological research (Garshelis, 2000) and aid reserve selection both at a small scale and in the wider landscape (Araújo, Williams & Fuller, 2002; Bani *et al.*, 2002). Habitat suitability models have also been used to estimate the effect of climate change (Austin *et al.*, 1996; Buckland, Elston & Beaney, 1996). Finally, because birds are important indicators of ecosystem health (Furness & Greenwood, 1993), habitat suitability models may guide monitoring programmes.

Here we use a geographic information system to determine whether readily available spatial data can successfully describe Madagascar plover distribution and produce a predictive spatial model. In order for this to be possible, the species must be sufficiently habitat specific to show a significant relationship with remotely sensed environmental data (Dembinski, Kindscher & Jakubauskas, 1999). We then use the habitat suitability model to estimate population size on the basis of the predicted area of suitable habitat and the known density of Madagascar plovers in suitable sites. This approach is particularly relevant in countries such as



Madagascar where the road system is poor, so that many wetland birds have never been surveyed thoroughly.

## Methods

In the field, we only collected presence data, because the logistical difficulty of repeatedly visiting sites to verify absence made it impossible to collect a reliable absence dataset. Some authors have suggested that when true absence data have not been collected, distribution models may be produced based on presence data and randomly generated pseudo-absences (Osborne, Alonso & Bryant, 2001; Stockwell & Peterson, 2002); however, Boyce *et al.* (2002) suggest that this approach may result in bias in the absence data if the species has a wide range or there are relatively few presence points. Instead, we use ecological niche factor analysis (ENFA), which only requires a set of presence points. Brotons *et al.* (2004) caution that the lack of absence data prevents suitable areas being restricted by the species' environmental limitations, although Zaniwski, Lehmann & McOverton (2002) argue that presence-only methods generate distributions that best reflect the species' fundamental niche.

The niche concept, defined by Hutchinson (1957), considers a species' ecological niche to be a hypervolume in the multidimensional space defined by information about environmental variables, within which the species can persist. ENFA has been developed to analyse the position of the niche of a species in the wider ecological space of the environment (Hirzel *et al.*, 2002). In ENFA, the niche of a species relative to the environment is described by extracting an axis of marginality (a vector from the average of available habitat characteristics to the average of used habitat characteristics). The analysis then extracts successive uncorrelated orthogonal axes maximizing the specialization of the species. Having described the niche of a species, it is then possible to predict the probability that each unit of the landscape, with associated habitat characteristics, is suitable habitat for the focal species.

## Fieldwork and data collection

The historical range of the Madagascar plover is from the Mahavavy delta in the north to Fort Dauphin in the south-east (Milon, 1950; Appert, 1971; Hayman, Marchant & Prater, 1986). Despite extensive surveys, Madagascar plover have never been sighted along the limestone coastline north of the Mahavavy delta (S. Goodman, pers. comm.). We collected data on the distribution and abundance of Madagascar plover during 8 months of fieldwork over 3 years between March 2003 and May 2005 throughout this historical range. Thirty-five wetland sites representing the range of wetland habitats present in western Madagascar across the whole range of the Madagascar plover were selected using 1:500 000 Foiben-Taosarintanin'i Madagaskara topographic maps. In some cases, site selection was constrained by logistical limitations, in particular the poor

condition of most roads in the region. All data were collected in the field by S. Z.

At each site, Madagascar plovers were counted, and the exact location where each bird was sighted was recorded with a GPS receiver (Garmin e-Trex, Olathe, KS, USA). Of 35 sites surveyed, 21 contained Madagascar plovers, and we collected the co-ordinates of 162 presence points. The area of habitat homogenous with the points at which Madagascar plover were sighted was estimated at each study site by considering each habitat patch in each site as a rectangle, estimating the lengths and widths (in m) in the field, and then calculating the area of each rectangular patch and summing all patches in each site.

All presence points were plotted in the UTM 38S reference system using the WGS1984 datum. This point shapefile was converted to a raster grid with the same dimensions as the environmental datasets. We then created 100 m buffers around these points to describe the environment in the birds' immediate vicinity, generating a set of cells that are used by Madagascar plovers. These were then made into a Boolean raster in which the presence cells were coded as 1 and all other cells received a value of 0.

## Ecogeographical variable (EGV) maps

Owing to the large size of our study area, and our aim of modelling habitat selection by Madagascar plovers at the finest possible scale, we selected Landsat 7 data because they have a relatively high spatial and good spectral resolution and are readily available for our study area. We used 17 Landsat 7 scenes acquired in summer 2000, 2001 and 2002 (Table 1). The source for this dataset was the Global Landcover Facility (<http://www.landcover.org>). These images were selected because all were collected during the dry season and all have negligible cloud cover. Owing to our large study area, it was not possible to find a set of images collected in the same year that were free of cloud cover.

Bands 1, 2, 3, 4, 5 and 7 were mosaiced separately and the mosaics were then clipped to within the west coast of Madagascar to produce six coverages of our study area, a total area of 242 445 km<sup>2</sup> (Fig. 1). All image processing work used Idrisi Kilimanjaro (Eastman, 2003).

The tasseled cap transformation (Kauth & Thomas, 1976) is a robust vegetation index that may be used with six bands of Landsat Enhanced thematic mapper plus (ETM+) data (Crist & Ciccone, 1984). This method exploits correlations between the bands in a multispectral Landsat image and allows the principal axes in hyperdimensional band space to be visualized easily. We used a tasseled cap transformation using coefficients for the Landsat ETM+ sensor (Huang *et al.*, 1998) to reduce the number dimensions of reflectance data and extract biologically meaningful environmental indices. This produced three rasters: tasseled cap greenness shows the amount of green vegetation, tasseled cap moistness describes the amount of water and tasseled cap brightness summarizes soil characteristics (Fig. 2). Finally, all three transformed images were rescaled such that pixels took digital number values from 0 to 255.

**Table 1** Landsat scenes used in this study

Path/row (WRS #)	Date	Sensor	Landsat #	ID
p158r077 (WRS 2)	13 September 2001	ETM +	Landsat 7	L7CPF20010701_20010930_05
p159r078 (WRS 2)	11 July 2001	ETM +	Landsat 7	L7CPF20011001_20011231_05
p159r077 (WRS 2)	28 May 2000	ETM +	Landsat 7	L7CPF20000401_20000630_09
p160r071 (WRS 2)	24 September 2000	ETM +	Landsat 7	L7CPF20000719_20000930_10
p160r072 (WRS 2)	23 April 2002	ETM +	Landsat 7	L7CPF20020401_20020630_03
p160r073 (WRS 2)	4 April 2001	ETM +	Landsat 7	L7CPF20010401_20010630_06
p160r074 (WRS 2)	23 April 2002	ETM +	Landsat 7	L7CPF20020401_20020630_03
p160r075 (WRS 2)	4 April 2001	ETM +	Landsat 7	L7CPF20010401_20010630_06
p160r076 (WRS 2)	1 April 2000	ETM +	Landsat 7	L7CPF20000401_20000630_09
p160r077 (WRS 2)	6 May 2001	ETM +	Landsat 7	L7CPF20010401_20010630_06
p161r071 (WRS 2)	8 April 2000	ETM +	Landsat 7	L7CPF20000401_20000630_09
p161r072 (WRS 2)	27 June 2000	ETM +	Landsat 7	L72161072_07220000627_B80
p161r073 (WRS 2)	4 February 2000	ETM +	Landsat 7	L72161073_07320000204_B80
p161r074 (WRS 2)	27 June 2000	ETM +	Landsat 7	L7CPF20000401_20000630_09
p161r075 (WRS 2)	23 March 2000	ETM +	Landsat 7	L7CPF20000101_20000331_11
p161r076 (WRS 2)	27 June 2000	ETM +	Landsat 7	L72161076_07620000627_B80
p161r077 (WRS 2)	30 April 2002	ETM +	Landsat 7	L7CPF20020401_20020630_03

ETM+, Enhanced thematic mapper plus.

Elevation data were derived from the Shuttle Radar Topography Mission (SRTM). Tiles of SRTM data corresponding to the 17 WRS-2 scenes of Landsat data used (Table 1) were downloaded from the Global Landcover Facility (<http://www.landcover.org>). These were then mosaiced and clipped in the same way as the satellite images. The resolution of this dataset was 90 m, but in order to overlay all layers of environmental data exactly, we re-sampled the SRTM to 30 m resolution to produce the final elevation map (Fig. 2). Elevation in the study area ranges from 0 to 1625 m.

As a *proxy* measure of human impact, we made a raster in which each cell took as its value the distance (km) to the nearest settlement. A point shapefile containing all settlements in Madagascar was projected to UTM 38S and clipped to the study area plus a 50 km buffer to eliminate edge effects. The source of this data was <http://www.gospa-tial.com>. This shapefile was then converted to a 30 m raster in which cells containing a settlement were coded 0 and all others were coded 1. The distance (in km) from every cell to the nearest settlement was then calculated and each cell took a value 0–54.9 km. Finally, this raster was clipped to the study area to produce a map that could exactly overlay the other environmental datasets (Fig. 2).

Because the Madagascar plover appears to be dependent on coastal habitats, we created a raster in which each cell took as its value the distance to the coast. To create this, the coastline shapefile used to define the study area was converted to a 30 m raster with the same extent as the other environmental datasets. Coastal cells were coded 1 and all other cells were coded 0. The distance (in km) from every cell to the coast was then calculated and each cell took a value 0–259.6 km. Finally, this raster was clipped to the study area to produce the coast distance map (Fig. 2).

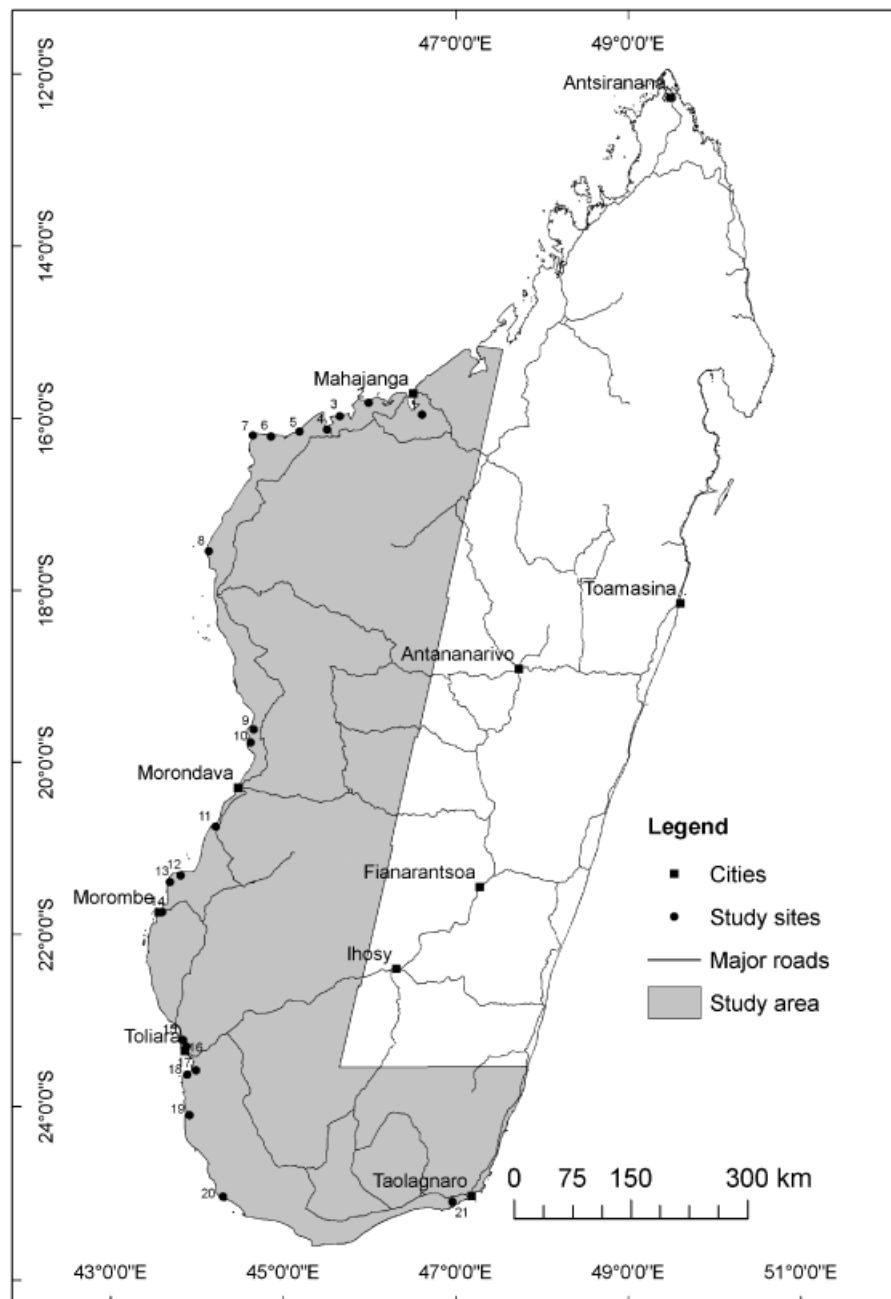
## Habitat suitability modelling

The program Biomapper (Hirzel, Hausser & Perrin, 2004) was used for all habitat suitability modelling. We prepared all EGV maps for Biomapper using a Box-Cox transformation to *normalize* the distribution of values in each map (Sokal & Rohlf, 1994).

Following Hirzel & Arlettaz (2003), we then used the distance geometric mean algorithm in Biomapper to predict habitat suitability across the landscape because this algorithm is designed to have high generalization power and it makes no assumption about the frequency distribution of Madagascar plover presence points with respect to the values in each EGV dataset. The resultant habitat suitability maps produced by Biomapper are a spatial representation of habitat suitability values (0–100%) calculated for every 30 m cell in the study area ( $n = 384\,833\,342$  cells).

We repeated the habitat suitability modelling process twice. First, we used *k-fold partitioning* with 10 sets to allow model validation using a receiver operating characteristic (ROC) plot and to also estimate the mean frequency and standard error of area of habitat predicted to fall within each suitability class across 10 different runs of the model (Boyce *et al.*, 2002). Data were partitioned by site and then individual presence cells were selected. This procedure minimized the potential for spatial pseudo-replication. Second, we used all available presence data to produce a final habitat suitability model as recommended by Fielding & Bell (1997).

To validate our model, we produced a ROC plot. Because false positives (where suitable habitat is predicted in areas where no presence data have been collected) provide no information about the quality of this model, standard validation estimators such as the  $\kappa$  index (Monserud & Leemans, 1992), which give the same importance to false positives and false negatives (when unsuitable habitat is

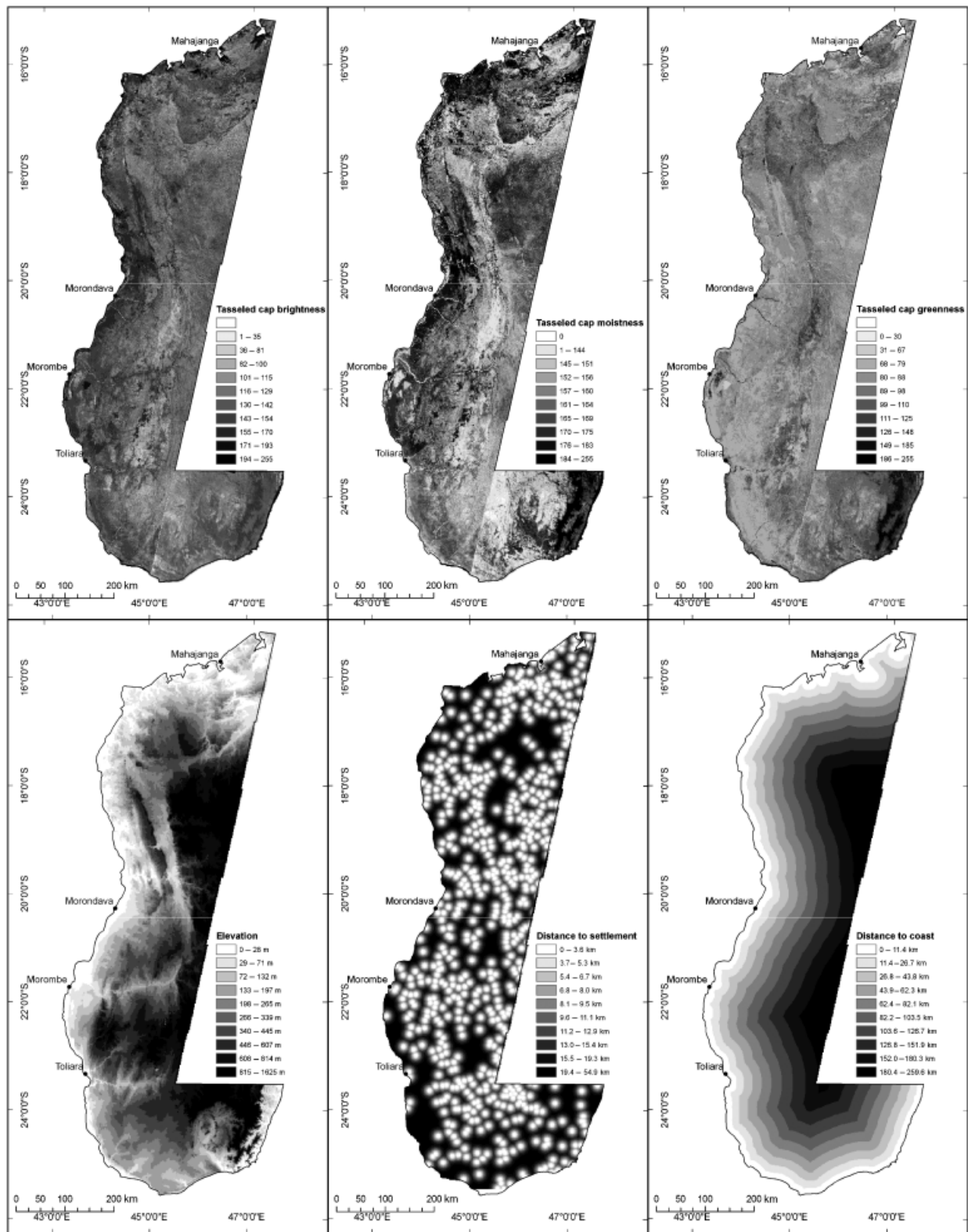


**Figure 1** Location map. The shaded area of western Madagascar represents the study region. Study sites are marked by open circles, and major cities by solid circles.

predicted in areas where the species is present), could not be used (Pearce & Ferrier, 2000). The area under the ROC curve (AUC) provides a measure of the overall accuracy of the model that is independent of any particular threshold. The value of AUC ranges between 0.5 and 1.0. A score of 0.5 indicates a model that performs no better than chance, whereas a model scoring 1.0 fits the data perfectly.

Many studies that generate a habitat suitability map pick an arbitrary threshold such as 50 or 70% and state that

all habitats above the threshold are suitable and all habitats below are unsuitable. However, this approach is arbitrary and has no biological justification. Instead, we estimated the success of our model across the full range of possible thresholds using an ROC plot, and determined the most appropriate threshold from a 45° tangent to the ROC curve that assumes an equal risk of false-positive and false-negative predictions (Zweig & Campbell, 1993).



**Figure 2** Six ecogeographical variable maps used to explain Madagascar plover distribution.

**Table 2** Variance explained by the four marginality and specialization factors calculated by ecological niche factor analysis (ENFA)

EGV	Marginality factor (59%)	EGV	Specialization factor 1 (17%)	EGV	Specialization factor 2 (8%)	EGV	Specialization factor 3 (4%)
Elevation	-0.90	Tasscap moist	0.51	Tasscap bright	0.40	Tasscap green	0.29
Tasscap moist	0.57	Elevation	0.48	Tasscap bright	0.23	Tasscap green	0.16
Tasscap bright	0.35	Tasscap green	0.27	Elevation	0.15	Tasscap moist	0.09
Tasscap green	0.17	Tasscap bright	0.13	Tasscap moist	0.05	Elevation	0.03

A positive marginality coefficient indicates that Madagascar plover presence points have higher values of this EGV than the median of the whole study area, whereas a negative coefficient indicates that Madagascar plovers prefer areas with lower values of the EGV than generally found in the environment. The amount of marginality or specialization accounted for by each factor is given in parentheses.

EGV, ecogeographical variable.

### Estimating population size from the habitat suitability model

First, we measured the area of suitable habitat for Madagascar plovers by plotting a histogram of the final habitat suitability map, using standard errors (SES) derived from *k*-fold partitioning to describe the uncertainty in these estimates. Our habitat suitability threshold, the value above which habitat supports Madagascar plovers (determined from the ROC plot), then allowed us to consider only the area of habitat predicted to be more suitable than the threshold.

Second, we estimated the density and standard error of Madagascar plovers in each study site (suitable habitats). Having tested for normality, we then estimated the mean density and SE of Madagascar plovers across all sites. Following the logic of Mladenoff & Sickley (1998), we then multiplied this density by the area of suitable habitat to estimate the total population size and its SE.

### Results

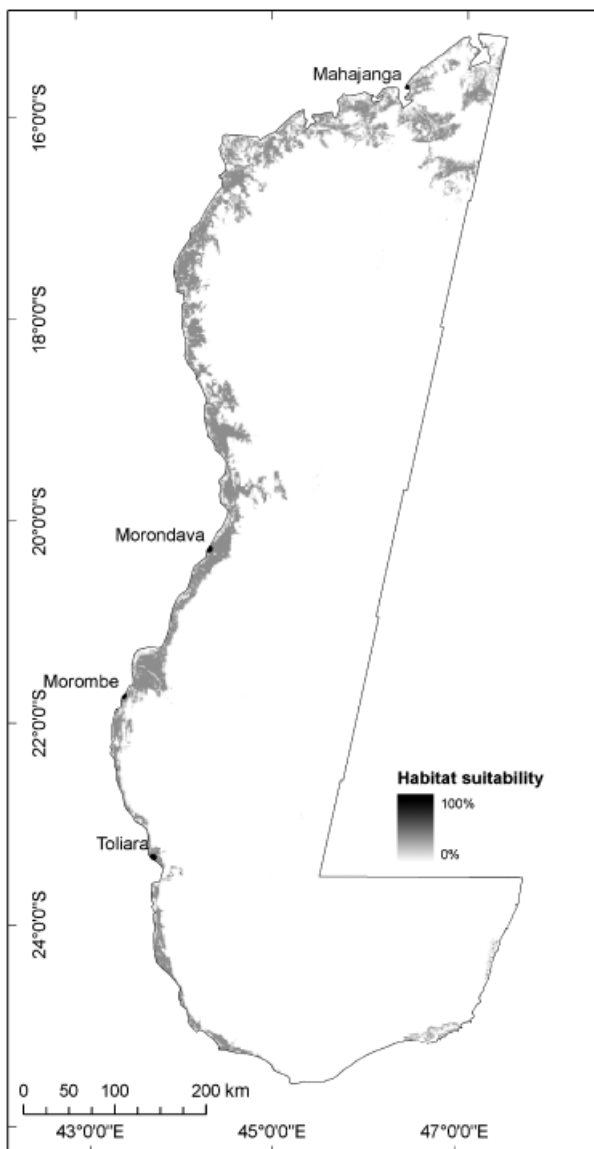
Our surveys found 263 plovers in the dry season (April–November) and 370 individuals in the wet season (December–March) in 21 sites between August 2003 and March 2005 (Fig. 1).

#### Habitat suitability model

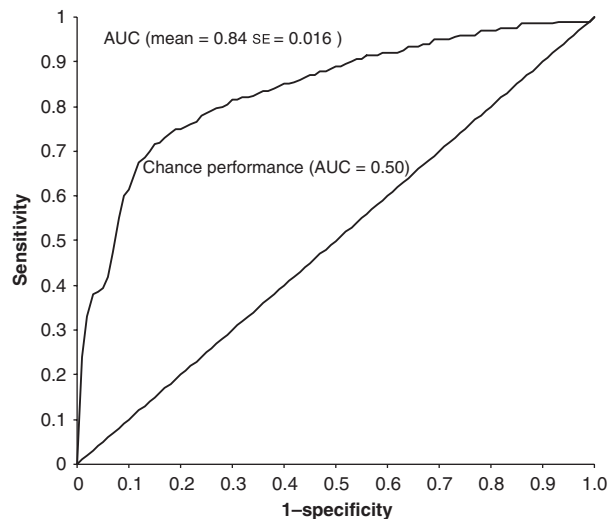
Of six EGVs, two were removed before the final model was produced. Coast distance was removed because it was highly correlated with elevation, and conferred no explanatory power to the model. Settlement distance was also removed because it did not significantly explain variation in Madagascar plover presence.

The four EGVs used to make the final model were tasseled cap brightness, tasseled cap moistness, tasseled cap greenness and elevation (Table 2). Marginality coefficients showed that, relative to the study area as a whole, Madagascar plovers prefer sites with low elevation (elevation = -0.90) and higher moistness (tasseled cap moistness = 0.57), brightness (tasseled cap brightness = 0.35) and greenness (tasseled cap greenness = 0.17).

The final habitat suitability model shows many patches of varying levels of habitat suitability along the west coast of

**Figure 3** Final habitat suitability model.

Madagascar, with smaller suitable areas on the south-east coast. However, the most suitable areas are fragmented from each other by less suitable habitat (Fig. 3).



**Figure 4** Receiver operating characteristic plot of training and validation data. Sensitivity is the true positive fraction, and 1-specificity is the false-positive fraction for each unique threshold in the data. The diagonal line represents model performance that would be expected by chance alone.

### Model validation

The model performed well in predicting Madagascar plover presence when evaluated with an ROC plot (AUC mean = 0.84, SE = 0.016, Fig. 4). This suggests that in the final model, a cell predicted as suitable habitat, at any threshold of suitability, will be more suitable than a randomly selected cell in the study area at least 84% of the time.

### Madagascar plover population estimate

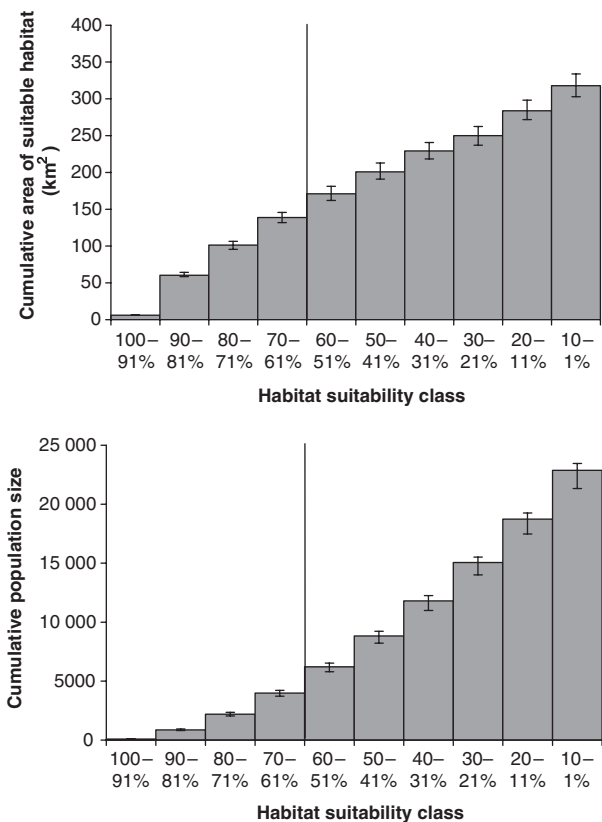
As estimated from the tangent to the ROC curve, the threshold value of habitat suitability (scaled 0–100%; Fig. 3) above which Madagascar plovers use the habitat was 61%. Only cells that predicted a habitat suitability value greater than, or equal to, this threshold were considered to be suitable.

The total area of habitat more suitable than the threshold was  $139 \pm 6 \text{ km}^2$  (mean  $\pm$  SE, Fig. 5). The mean density of Madagascar plovers in suitable habitat was  $0.13 \pm 0.03 \text{ ha}^{-1}$  (Table 3). Integrating the area under the cumulative population size histogram (Fig. 5), we estimate the total population of Madagascar plovers to be  $3100 \pm 396$  individuals.

## Discussion

### Habitat suitability model

Like other large-scale habitat suitability modelling studies, our choice of EGVs was limited by the available environmental data (Luck, 2002; Gibson *et al.*, 2004). In the trade-off between a model with fine-scaled habitat variables that would predict across a limited area versus a potentially less



**Figure 5** Cumulative area of suitable habitat and cumulative Madagascar plover population estimates in each habitat suitability class. Error bars on the histogram of cumulative area represent standard errors from 10-fold partitioning. The error bars on the histogram of cumulative population represent standard errors in the estimate of area and Madagascar plover density. The vertical bars mark the threshold value (61%) above which habitat is suitable.

accurate model that could be generalized across western Madagascar, we elected for a broad model. There is scope, however, to refine this model by incorporating finer scale data from intensively surveyed sites to better understand the threats to the Madagascar plover.

In this study, it was necessary to validate the model by partitioning the dataset. Ideally, model validation will involve a comparison with independent data, although with rare species such as the Madagascar plover, this is often not available. However, the collection of further data in future studies will allow a fuller assessment of the adequacy of this model.

The habitat suitability model was created using a single snapshot of environmental data. In reality, the coast of western Madagascar is dynamic and sudden changes in habitat conditions may occur after natural events such as cyclones. This would result in individuals being displaced into lower quality habitats (Gates & Donald, 2000). In general, it is reasonable to assume, due to the dispersal ability of birds, that the Madagascar plover is in close equilibrium with the environment, regulated by habitat

**Table 3** Density of Madagascar plovers in suitable sites

ID	Site	Area of suitable habitat (ha)	Number of Madagascar plovers	Density (ha <sup>-1</sup> )
1	Mahavavy delta	98	8	0.08
2	Bombetoka bay	200	4	0.02
3	Marambitsy bay	655	86	0.13
4	Baly bay national park	1980	92	0.05
5	East Antilohy bay	35	14	0.40
6	West Antilohy bay	228	8	0.04
7	Cap Sainte André	703	6	0.01
8	Tambohorano	60	6	0.10
9	Besalampy	160	19	0.12
10	Tsiribihina delta	150	21	0.14
11	Belo sur mer	8000	40	0.01
12	Morombe	314	20	0.06
13	South Mangoky delta	25	6	0.24
14	North Mangoky delta	292	27	0.09
15	Toliara airport	32	10	0.31
16	Mangily/Ifaty	80	9	0.11
17	Soalany	25	1	0.04
18	Mozambika/Manambolo	10	2	0.20
19	Lake Tsimanampetsotse	650	133	0.20
20	Androkaela	175	29	0.17
21	Antamboho	60	14	0.23

Site numbers correspond to the legend in Fig. 1.

selection and population dynamics (Chamberlain & Fuller, 1999). Furthermore, Miller *et al.* (1989) argue that some sacrifice of precision is acceptable in analysis such as this for the sake of the generality and conservation usefulness of the predictions that can be made on the basis of observed species–habitat associations.

It is interesting that distance to settlement had no effect on habitat suitability because human activities likely to affect Madagascar plovers, for instance grazing by zebu *Bos indicus*, help to maintain an appropriate sward height in saltmarshes for plovers to feed and nest. Nonetheless, these impacts could still be harmful if trampling would increase mortality of nests and/or chicks, and the intensity of disturbance increases as a result of increased human migration to the coastal zone.

### Madagascar plover population estimate

There are several factors other than modelled habitat suitability that may affect Madagascar plover presence/absence in the areas predicted to be suitable (Flather *et al.*, 1997).

First, historical events such as large-scale colonization and long-term persistence affect whether the species can occur in some areas predicted to be suitable. For example, an isolated patch of suitable habitat may never be colonized (Ricklefs, 2004). Second, metapopulation dynamics may cause some patches of suitable habitat to not support a population of plovers sometimes (Hanski, 1999). The effect of this on the Madagascar plover is difficult to quantify because its dispersal behaviour and seasonal movements are

not known. Third, competitive exclusion (Brown, 1984) by congeneric small plovers such as Kittlitz's plover *Charadrius pecuarius* and white-fronted plover *Charadrius marginatus* could make some areas unsuitable. Note that the latter two species co-occur with Madagascar plover, and all three species breed in several sites (Zefania *et al.*, submitted). Fourth, it is possible that hierarchical habitat selection (Winkler & Leisler, 1985) as a result of human threats, or specific habitat requirements at certain times of the year or parts of the life cycle (e.g. nesting), may further restrict the Madagascar plover within the areas predicted to be suitable by this model. Unfortunately, none of these factors can be measured by remote sensing; instead, models such as the present one must be refined by detailed follow-up fieldwork.

### Conservation applications

Currently, the Madagascar plover is classified as vulnerable. Our data suggest that it is close to being endangered using IUCN criteria (IUCN, 2001). The estimated area of occupancy is substantially less than the 500 km<sup>2</sup> threshold for listing under criteria B2; however, we do not have data on the trends in the extent of occurrence, area of occupancy, habitat quality, number of populations or numbers of mature individuals, which are also necessary to list under this criterion. Our estimated population size is also close to the 2500 mature individuals threshold of criterion C. The productivity of Madagascar plover is extremely low compared with temperate-zone congenics, and using productivity data from the stronghold of Madagascar plover at Lac Tsimanampetsotse, Zefania *et al.* (submitted) predicted rapid decline. Taken together, the specialized habitat requirements, small area of occupancy, low population size and declining population may justify elevating the Madagascar plover status to endangered.

Throughout the range, there are only 10 sites where Madagascar plover are known to breed: Androkaela, Antilohy bay, Besalampy, Fort-Dauphin, Ifaty, Mahavavy delta, Mangoky delta, Marambitsy bay, Lake Tsimanampetsotse and the Tsiribihina delta. Of these, the two most important breeding strongholds are at Lake Tsimanampetsotse and Marambitsy bay (Zefania *et al.*, in press). These sites are, therefore, high priorities for protection and appropriate management.

At present, there are few protected wetlands in the range of the Madagascar plover. These sites are Baly Bay National Park, Lake Tsimanampetsotse National Park and the new Kirindy-Mitea National Park. Additionally, temporary protection has been accorded to the Mahavavy-Kinkony area. These areas include the main breeding stronghold at Lake Tsimanampetsotse and confer some protection on Marambitsy bay. Although Madagascar plover occur in the Kirindy-Mitea area, breeding has not been recorded. Our habitat suitability model allows the areas of greatest importance to Madagascar plover to be identified for use in further protected area planning. In doing this, it is possible to adopt a conservative approach, selecting areas predicted in the highest habitat suitability. This approach assumes a

direct positive correlation between habitat suitability and density (Elith, Burgmann & Regan, 2002).

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## References

- Akçakaya, H.R. & Atwood, J.L. (1997). A habitat-based metapopulation model of the California Gnatcatcher. *Conserv. Biol.* **11**, 422–434.
- Appert, O. (1971). Die Limikolen des Mangokygebietes in Südwest-Madagascar. *Orn. Beob.* **68**, 53–77.
- Araújo, M.B., Williams, P.H. & Fuller, R.J. (2002). Dynamics of extinction and the selection of nature reserves. *Proc. Roy. Soc. Lond. Ser. B* **269**, 1971–1980.
- Austin, G.E., Thomas, C.G., Houston, P.C. & Thompson, P.B.A. (1996). Predicting the spatial distribution of buzzard *Buteo buteo* nesting areas using a geographic information system and remote sensing. *J. Appl. Ecol.* **33**, 1541–1550.
- Avery, M.I. & Haines-Young, R.H. (1990). Population estimates of dunlin (*Calidris alpina*) from remotely sensed imagery of the Flow Country of Northern Scotland. *Nature* **344**, 860–862.
- Bani, L., Baietto, M., Bottoni, L. & Massa, R. (2002). The use of focal species in designing a habitat network for a lowland area of Lombardy, Italy. *Conserv. Biol.* **16**, 826–831.
- BirdLife International (2004). *Charadrius thoracicus*. In *IUCN 2007. IUCN red list of threatened species*. <http://www.iucnredlist.org> accessed 12/11/07].
- Boyce, M.S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K.A. (2002). Evaluating resource selection functions. *Ecol. Model.* **157**, 281–300.
- Brotons, L., Thuiller, W., Araújo, M.B. & Hirzel, A.H. (2004). Presence-absence versus presence-only modeling methods for predicting bird habitat suitability. *Ecography* **27**, 437–448.
- Brown, J.H. (1984). On the relationship between abundance and distribution of species. *Am. Nat.* **124**, 255–279.
- Buckland, S.T., Elston, D.A. & Beane, S.J. (1996). Predicting distributional change with application to bird distributions in Northeast Scotland. *Global Ecol. Biogeogr. Lett.* **5**, 66–84.
- Chamberlain, D.E. & Fuller, R.J. (1999). Density-dependent habitat distribution in birds: issues of scale, habitat definition and habitat availability. *J. Avian Biol.* **30**, 427–436.
- Crist, E.P. & Cicone, R.C. (1984). Application of the tasseled cap concept to simulated thematic mapper data. *Photogram. Eng. Rem. Sens.* **50**, 343–352.
- Eastman, J.R. (2003). *Idrisi Kilimanjaro. Guide to GIS and image processing*. Worcester, MA, USA: Clark Labs.
- Dembinski, D.M., Kindscher, K. & Jakubauskas, M.E. (1999). A remote sensing and GIS-based model of habitats and biodiversity in the greater yellowstone ecosystem. *Int. J. Rem. Sens.* **20**, 3281–3291.
- Dettmers, R. & Bart, J. (1999). A GIS modeling approach to predicting forest songbird habitat. *Ecol. Appl.* **9**, 152–163.
- Durbin, J., Bernard, K. & Fenn, M. (2003). The role of socioeconomic factors in loss of Malagasy biodiversity. In *The natural history of Madagascar*: 142–146. Goodman, S.M. & Benstead, J.P. (Eds). Chicago: University of Chicago Press.
- Elith, J., Burgmann, M.A. & Regan, H.M. (2002). Mapping epistemic uncertainties and vague concepts in predictions of species distribution. *Ecol. Model.* **157**, 313–329.
- Fielding, A.H. & Bell, J.F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* **24**, 38–49.
- Flather, C.H., Wilson, K.R., Dean, D.J. & McComb, W.C. (1997). Identifying gaps in conservation networks: of indicators and uncertainty in geographic analysis. *Ecol. Appl.* **7**, 531–542.
- Furness, R.W. & Greenwood, J.J.D. (1993). *Birds as monitors of environmental change*. London: Chapman & Hall.
- Garshelis, D.L. (2000). Delusions in habitat evaluation: measuring use, selection and importance. In *Research techniques in animal ecology*: 111–164. Boitani, L. & Fuller, T.K. (Eds). New York: Columbia University Press.
- Gates, S. & Donald, P.F. (2000). Local extinction of British farmland birds and the prediction of further loss. *J. Appl. Ecol.* **37**, 806–820.
- Gibson, L.A., Wilson, B.A., Cahill, D.M. & Hill, J. (2004). Spatial prediction of rufous bristlebird habitat in a coastal heathland: a GIS based approach. *J. Appl. Ecol.* **41**, 213–223.
- Gottschalk, T.K., Huettmann, F. & Ehlers, M. (2005). Thirty years of analyzing and modeling avian habitat relationships using satellite imagery data: a review. *Int. J. Rem. Sens.* **26**, 2631–2656.



- Gratto-Trevor, C.L. (1996). Use of Landsat TM imagery in determining important shorebird habitat in the outer MacKenzie delta, Northwest Territories. *Arctic* **49**, 11–22.
- Guisan, A. & Zimmermann, N.E. (2000). Predictive habitat distribution models in ecology. *Ecol. Model.* **135**, 147–186.
- Hanski, I. (Ed.). (1999). *Metapopulation ecology*. Oxford: Oxford University Press.
- Hayman, P., Marchant, J. & Prater, T. (1986). *Shorebirds: an identification guide to the Waders of the World*. London: Christopher Helm Ltd.
- Hirzel, A.H. & Arlettaz, R. (2003). Modelling habitat suitability for complex species distributions by environmental-distance geometric mean. *Environ. Mgmt.* **32**, 614–623.
- Hirzel, A.H., Hausser, J., Chessel, D. & Perrin, N. (2002). Ecological-niche factor analysis: how to compute habitat suitability maps without absence data? *Ecology* **83**, 2027–2036.
- Hirzel, A.H., Hausser, J. & Perrin, N. (2004). *Biomapper 3.0*. Bern, Switzerland: Division of Conservation Biology, University of Bern. [<http://www.unil.ch/biomapper> accessed 12/08/06].
- Huang, C., Wylie, B., Yang, L., Homer, C. & Zylstra, G. (1998). *Derivation of a tasseled cap transformation based on Landsat 7 at-satellite reflectance*. Sioux Falls, SD, USA: Raytheon ITSS, USGS EROS Data Center. [<http://landcover.usgs.gov/pdf/tasseled.pdf> accessed 12/08/06].
- Hutchinson, G.E. (1957). Concluding remarks. *Cold Spring Harb. Symp. Quant. Biol.* **22**, 415–427.
- IUCN (2001). *International Union for the Conservation of Nature red list categories version 3.1*. Gland, Switzerland: IUCN.
- Kauth, R.J. & Thomas, G.S. (1976) The tasseled cap – a graphic description of the spectral temporal development of agricultural crops as seen by Landsat. *Proceedings of the symposium on machine processing of remotely sensed data*, Purdue University, West Lafayette, IN, pp. 41–51.
- Luck, G.W. (2002). The habitat requirements of the rufous treecreeper (*Climacteris rufa*). 2. Validating predictive habitat models. *Biol. Conserv.* **105**, 395–403.
- Miller, R.I., Stuart, S.N. & Howell, K.M. (1989). A methodology for analysing rare species distribution patterns: the rare birds of Tanzania. *Landscape Ecology* **2**, 173–189.
- Milon, P. (1950). Deux jours au lac Tsimanampetsotsa: observations ornithologiques. *Nat. Malgache* **2**, 61–67.
- Mladenoff, D.J. & Sickley, T.A. (1998). Assessing potential gray wolf restoration in the Northeastern United States: a spatial prediction of favourable habitat and potential wolf population levels. *J. Wildl. Mgmt.* **62**, 1–10.
- Monserud, R.A. & Leemans, R. (1992). Comparing global vegetation maps with the Kappa statistic. *Ecol. Model.* **62**, 275–293.
- Osborne, P.E., Alonso, J.C. & Bryant, R.G. (2001). Modelling landscape-scale habitat use using GIS and remote sensing: a case study with great bustards. *J. Appl. Ecol.* **38**, 458–471.
- Pearce, J. & Ferrier, S. (2000). An evaluation of alternative algorithms for fitting species distributions using logistic regression. *Ecol. Model.* **128**, 127–147.
- Ricklefs, R.E. (2004). A comprehensive framework for global patterns in biodiversity. *Ecol. Lett.* **7**, 1–15.
- Scott, J.M., Davis, F., Csuti, B., Noss, R., Butterfield, B., Groves, C., Anderson, H., Caicco, S., D'Erchia, F., Edwards Jr, T.C., Ulliman, J. & Wright, R.G. (1993). Gap analysis: a geographic approach to the protection of biological diversity. *Wildl. Monogr.* **123**, 1–41.
- Sokal, R.R. & Rohlf, F.J. (1994). *Biometry: principles and practice of statistics in biological research*. London: W. H. Freeman and Co.
- Stockwell, D.R. & Peterson, A.T. (2002). Controlling bias in biodiversity. In *Predicting species occurrences: issues of accuracy and scale*: 537–546. Scott, M.S., *et al.* (Eds). Washington: Island Press.
- Wetlands International (2006). *Waterbird population estimates*. 4th edn. Wageningen, the Netherlands: Wetlands International.
- Winkler, H. & Leisler, B. (1985). Habitat selection: behavioural aspects. In *Habitat selection in birds*: 436–477. Cody, M.L. (Ed.). San Diego: Academic Press.
- Zaniewski, A.E., Lehmann, A. & McOverton, J. (2002). Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. *Ecol. Model.* **157**, 261–280.
- Zefania, S., French-Constant, R.H., Long, P.R. & Székely, T. (in press) Breeding ecology and distribution of the threatened Madagascar plover *Charadrius thoracicus* *Ostrich*.
- Zweig, M.H. & Campbell, G. (1993). Receiver-operating-characteristic (ROC) plots: a fundamental evaluation tool in clinical medicine. *Clin. Chem.* **39**, 561–577.

### **Chapter 3** Ecological factors and human threats both drive wildfowl population declines

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#### **Details and extent of the contributions by authors**

**P.R. Long:** data collection, statistical analysis, manuscript writing (80%)

**T. Székely:** general editing of the manuscript, suggestions to improve the study (10%)

**M. Kershaw:** suggestions to improve the study (5%)

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## Introductory note

In this chapter we perform a phylogenetic comparative analysis to test whether population size, global range size and ecological, life-history and sexually-selected traits predict population trends in wildfowl. We also consider anthropogenic threats, and human impacts within the breeding and non-breeding ranges of each species.

Our phylogenetic hypothesis was based on a wildfowl supertree (Figuerola & Green, 2000). We had to set all branch lengths to be of equal length, as no information on branch lengths in this tree was available. We then performed a comparative analysis using the program CAIC (Purvis & Rambaut 1995) to calculate phylogenetically independent contrasts.

This approach has since been superseded by Phylogenetic Generalised Linear Models (PGLM) in which the full structure of the tree, including branch lengths, is used to compute a variance-covariance matrix which controls for phylogenetic non-independence in the dataset (Maddison & Madisson 2004). Thus, a phylogenetic term can be included in a standard generalized linear model at species level.

However, in this study we elected to use the independent contrasts approach, implemented in CAIC, as no information on branch lengths was available.

## References

- Figuerola, J. & Green, A.J. (2000). The evolution of sexual dimorphism in relation to mating patterns, cavity nesting, insularity and sympatry in the Anseriformes. *Funct. Ecol.* 14, 701–710.
- Maddison, W. P. & Maddison, D. R. 2004 MESQUITE: a modular system for evolutionary analysis, version 1.12. See <http://mesquiteproject.org>.
- Purvis, A. & Rambaut, A. (1995). Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Comp. Appl. Biosci.* 11, 247–251.

# Ecological factors and human threats both drive wildfowl population declines

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## Keywords

Anseriformes; wildfowl; phylogenetic comparative analysis; threat; population; life-history; sexual selection; human population density.

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## Abstract

Many wildfowl species are declining and 34 out of 159 extant species are globally threatened, some of which are the subject of specific conservation programmes. Here we investigate which factors predict declining population trends across 154 species of Anseriformes. First we show that there are proportionately fewer declining wildfowl populations in North America, Europe and Australasia than in south and central America, Africa and Asia. Second, we use phylogenetic comparative analyses to test whether population size, global range size and ecological, life-history and sexually-selected traits predict population trends. We also consider anthropogenic threats, and human impacts within the breeding and non-breeding ranges of species. Using phylogenetically independent contrasts we show that small population size and small global ranges are the most important intrinsic factors that predispose wildfowl species to declining populations. Many wildfowl are hunted but, contrary to expectation, hunting did not influence population trends. Declining populations were associated with high International Union for the Conservation of Nature (IUCN) threat category, although the relationship is not very strong ( $r = 0.134$ ,  $n = 129$  contrasts) possibly because the IUCN criteria integrate population size, range size and an assessment of threat. Two extrinsic factors were significant predictors of population declines: the increase in area of agricultural land within a species' range (an indirect measure of wetland loss), and the total number of different threat processes such as habitat loss and pollution that threaten a species. Taken together, our results strongly suggest that both anthropogenic threats and intrinsic ecological factors are influencing population declines in wildfowl.

## Introduction

Globally, many of the 159 species of Anseriformes (ducks, geese, swans and screamers) are declining and 21% of these are currently threatened with extinction (Wetlands International, 2002). Extinction risk within avian taxa is not randomly distributed (Bennett & Owens, 1997). Across all birds several candidate factors have been identified to explain these extinction risk patterns; range sizes (Blackburn & Gaston, 2002); ecological traits such as habitat elevation (Gage *et al.*, 2004); life-history traits such as large body size and small clutch size (Arnold & Owens, 2002) and sexually selected traits such as large relative testes mass (Morrow & Pitcher, 2003).

Fisher & Owens (2004) argue that although taxonomically broad studies are effective in determining general correlates of extinction risk, studies which focus on a smaller taxonomic group will be more effective in identifying interactions between intrinsic and extrinsic factors responsible for population declines. In this paper we use wildfowl, a group that shows considerable diversity in ecology, life-

history and habitat use to investigate the influence of these factors on population trend over time.

Anseriformes are excellent indicator species for the health of wetlands (Furness & Greenwood, 1993). Wetlands are highly productive, diverse globally distributed ecosystems, but are threatened by a number of processes including drainage and conversion to agricultural land, over-harvesting of natural resources, changes to the hydrological regime, pollution and invasive species (Moser *et al.*, 1996).

Both intrinsic (i.e. ecological and life-history) and extrinsic (i.e. human-induced) effects may be involved in population declines. First, a species' population size and range size are likely to be important predictors of population trend as small populations will be more threatened due to demographic stochasticity, the risk of catastrophes and inbreeding (Gaston, 1994; Simberloff, 1998; Briskie & Mackintosh, 2004). Of course, it is possible that small population size and ranges are emergent properties of declining populations, but it is not possible for us to test this causality.

Second, species at higher trophic levels – higher up the food chain – may be expected to have a more adverse

population trend than species at a lower trophic level at a given level of anthropogenic pressure as a result of vulnerability to 'chains of extinction' effects (Diamond, 1984), and the need for lower population densities. Migratory species may be more threatened as a result of high site fidelity and dependence on two separate areas in which they may be at risk from anthropogenic changes to the landscape (Pimm, Jones & Diamond, 1988). However a migratory habit may also confer greater dispersal ability and adaptability to different environments, which may buffer the species from other threats (Green, 1996).

Third, life-history traits such as large body size, small clutch size, delayed sexual maturity, which are associated with more K-selected slow life-histories, may predispose a species to decline (Pimm *et al.*, 1988; Gaston & Blackburn, 1995). This results from a decreased ability to increase fecundity to compensate for increases in adult mortality in the population.

Fourth, intense sexual selection is considered to increase extinction risk (Moller, 2000). Kokko & Brooks (2003) argue that strong sexual selection causes species to evolve traits which increase mating opportunities, but at a fitness cost which compromises survival. Morrow & Pitcher (2003) found that only post-mating sexual selection (sperm-competition) is correlated with increased extinction risk in birds, and that pre-mating sexual selection is not associated with elevated threat status.

Finally, humans may threaten a species in a variety of ways, such as habitat modification, hunting and introducing alien species to an ecosystem. Unfortunately, it is difficult in most cases to directly measure human impacts on a species. Instead, one may identify indices of human activity, which coincide in space and time with the population trend in the species of interest. Thus, *proxy* measures such as human population density within each species range were used. Cardillo *et al.* (2004) found human population density within carnivore ranges predict conservation status. However, other measures of human impact such as number of households (Liu *et al.*, 2003) may be more suitable.

Green (1996) examined the impacts of intrinsic and extrinsic factors on wildfowl, but without controlling for the effects of phylogeny. It is not appropriate to treat values of traits from closely related species as independent since such traits are often shared through common descent rather than independent evolution. Phylogenetic comparative methods allow comparisons to be made by examining independent evolutionary events. Other workers have considered the effects of phylogeny, but have not incorporated extrinsic factors into their analyses of threatened wildfowl (Gaston & Blackburn, 1996). Furthermore, almost all previous studies of factors affecting the conservation status of a taxon have adopted International Union for the Conservation of Nature (IUCN) categories ('Red Lists', ranging from extinct to least concern) as a response variable. Unless this effect is controlled for by excluding species listed under the criteria from certain analyses, this can introduce the problem of logical circularity into any analysis of whether factors such as range size explain variations in conservation

status, as population size, rate of decline and range size have been used to derive the IUCN categories (IUCN, 2001).

In order to avoid this potential pitfall, we use population trend as our response variable. Population trend is an emergent property of natural populations that may be observed (Kunin & Gaston, 1997). We argue that population trend is a more independent measure of conservation status than IUCN categories. However, it is important to note that population trend, unlike the IUCN categories, does not necessarily equate to extinction risk. It is possible for a large population to have a slowly decreasing trend yet not have its persistence seriously threatened. Conversely, in extreme circumstances it is possible for a species assessed by IUCN criteria to be highly threatened, to have a stable or even increasing population trend, although only if its population size was lower than the threshold for listing in an IUCN category under criterion D (population size).

In this study we use phylogenetic comparative analyses to identify the factors that make some wildfowl species more threatened than others. We ask how intrinsic aspects of a species' biology and extrinsic human influences within a species' range contribute to the population trend of wildfowl. We assess the relative importance of population size and range, ecological traits, life-history traits and sexually selected traits. We also consider anthropogenic threat processes, and human impacts in the global range of each species. In addition, we test whether intrinsic biological traits make species more susceptible to extrinsic threats. Duncan, Blackburn & Worthy (2002) explored this interaction in relation to island birds, here we apply this approach across an order of birds.

## Methods

We used data from Waterbird Population Estimates (WPE, Wetlands International, 2002) on population size and population trend of 458 populations of 161 species of ducks, geese, swans and screamers (Anseriformes) as listed in Monroe & Sibley (1993). Bird handbooks were the major sources for the database of ecological, life-history and sexually selected characteristics (Brown, Urban & Newman, 1982; Cramp & Simmons, 1984; Marchant & Higgins, 1990; Del Hoyo, Elliot & Sargatal, 1992; Poole & Gill, 1995). The database and accompanying references are available in the electronic appendix.

## Species data

Population trend was represented by 1 = extinct; 2 = decreasing; 3 = stable or fluctuating; 4 = increasing (Wetlands International, 2002). The stable and fluctuating classes were pooled because of the small number of fluctuating populations ( $n = 8$  populations). Mean population trend for each species was calculated from the trends of all its populations, weighted by the size of each population size. The IUCN Red List category (Mace & Stuart, 1994) of each species was obtained from [www.redlist.org](http://www.redlist.org).

The IUCN category is a procedure for assessing the relative probability of extinction of species according to the level of their threat. We scored the IUCN category as: 1 = extinct (EX); 2 = critically endangered (CR); 3 = endangered (EN); 4 = vulnerable (VU); 5 = near threatened (NT); 6 = least concern (LC).

For each species, all population sizes reported in WPE were summed to obtain a total world population size. Global extents of occurrence (in km<sup>2</sup>) were obtained from Threatened Birds of the World (TBW, BirdLife International, 2004). Both population size and global extent of occurrence were natural log-transformed before analysis.

Stevens's modification of Rapoport's rule states that toward the equator, the mean sizes of species' ranges become smaller (Stevens, 1989) and Gaston & Blackburn (1996) demonstrate that Anseriformes indeed have larger ranges at higher latitudes. In order to control for the effect of latitude on global extent of occurrence, the latitude of each species' breeding range was scored, based on the midpoint of their ranges. We elected to use broad categories instead of a continuous variable due to the coarse scale of our breeding range data. The following scores were used: 1 = polar, north of 60°N or south of 60°S; 2 = temperate, between 60°N and the Tropic of Cancer 23°27'N or between the Tropic of Capricorn 23°27'S and 60°S; 3 = equatorial, between the Tropics of Cancer and of Capricorn. Following Dunn, Whittingham & Pitcher (2001), migratory status was scored using a three-point scale: 1 = sedentary, individuals move <100 km between breeding and non-breeding areas; 2 = partial migrant, individuals move 100–1000 km between breeding and non-breeding areas; 3 = full migrant, individuals move >1000 km between breeding and non-breeding areas.

To quantify habitat generalism, eight broad habitat types were identified following Green (1996): forest, marine, lake wetlands, river wetlands, grasslands, arable land, tundra and scrub. Categorical variables which could take a value of 1 = used or 0 = unused were created for each habitat type, and thus the habitat types of each species were recorded. Summing habitats used for each species yielded a habitat score. Habitat generalism was represented on an eight-point scale from 1 = one habitat type used, through 8 = eight habitat types used.

In order to score trophic level, a text description of the foods eaten by each species was prepared. The species list was then randomized and three observers scored these descriptions blindly to species identity, using the following scale: 1 = 81–100% animal matter; 2 = 61–80% animal matter; 3 = 41–60% animal matter; 4 = 21–40% animal matter; 5 = 0–20% animal matter.

Adult male mass (in grams) and adult female mass (in grams) were used to calculate a mean adult mass. Adult mass was natural log transformed before the analyses. Fecundity is the mean clutch size of each species.

We used two *proxies* of sexual selection. Sexual dimorphism was calculated as  $\log(\text{adult male mass}) - \log(\text{adult female mass})$ . Data on testes mass (in grams) were obtained from Dunn *et al.* (2001). Testes mass acts as a *proxy*

measurement of sperm-competition (post-mating sexual selection). As large animals tend to have larger testicles, male size was controlled in multiple regressions against population trend using body mass as a predictor variable.

We used dummy variables to score whether or not the following processes threatened each species: habitat loss/destruction; hunting; pollution; human disturbance; accidental human-induced mortality (Todd, 1996). Summing across these variables produced a score between 0 and 5 for total number of different threat processes.

To assess the degree of human impact on each species, a list was made of countries in each species' global range (range states). For each country we collected the following information: area (in km<sup>2</sup>), human population in both 1980 and 1990 (United Nations Population Division, 2004). We also collected data on annual water consumption/capita in 1990 as a *proxy* for pressures on wetlands (Gleick, 1998), and the area of agricultural land in 1980 and 1990, to allow the change in area of agricultural land to be measured over that time period by calculating the difference between the area of agricultural land in 1990 and in 1980. We believe the latter measure represents the degree to which wetlands have been lost to farmland (Food and Agriculture Organisation of the United Nations, 2005). Where possible measures of human impact were obtained for 1990, as this leaves a 10-year lag before the estimation of population trends.

Mean human population density (HPD, people × km<sup>-2</sup>) in 1990, per capita water consumption in 1990, and area of agricultural land in 1980 and 1990 across all countries in each species' range was calculated, weighted by area of country. This procedure assumes that countries form a part of a species' range proportional to their area. HPD in 1990, water consumption per capita in 1990, area of agricultural land in 1980 and area of agricultural land in 1990 were log transformed before analysis.

## Phylogenetic comparative analyses

We used bivariate and multiple least squares linear regression through the origin of phylogenetically independent contrasts (Felsenstein, 1985; Garland, Harvey & Ives, 1992). For most biological traits it is necessary to control for the effects of shared evolutionary history, since data from closely related species cannot be considered to be independent (Freckleton, Harvey & Pagel, 2002; Blomberg, Garland & Ives, 2003). This is as a result of evolutionary change in sister taxa of traits at a rate proportional to time as divergence (branch length) under a Brownian motion model of evolution (Harvey & Pagel, 1991). CAIC (Purvis & Rambaut, 1995) was used to estimate phylogenetically independent contrasts. We used R 2.1.0 (Ihaka & Gentleman, 1996) for statistical analyses.

Our phylogenetic hypothesis was based on a wildfowl supertree (Figuerola & Green, 2000). We set all branch lengths to equal lengths, as no information on branch lengths was available. The phylogenetic tree was pruned to remove taxa not recognized by Monroe & Sibley (1993). Three species of screamers (Anhimidae) were added to the

base of the phylogeny following Livezey (1986). Thus, there are a total of 154 species in our phylogeny.

We ensured heterogeneity of variance in the contrasts generated by CAIC before further analysis, as recommended by Garland *et al.* (1992). We plotted the contrasts in the explanatory variable against the standard deviation of the contrasts. We also tested for significant correlation between the contrasts and their standard deviations as recommended by the CAIC manual, but none were significant.

### Multiple regression model

Following bivariate analyses of phylogenetically independent contrasts, a saturated multiple regression model of population trend (response variable) was constructed using all significant ( $P < 0.05$ ) and near-significant ( $P < 0.1$ ) explanatory variables.

A minimum adequate model (MAM) was found by successive removal of the least significant term from the multiple regression model until in the MAM all terms were significant. We were unable to use the Akaike information criterion (AIC) to distinguish between competing models since degrees of freedom were different between models due to missing data (Burnham & Anderson, 2002). We also tested first-order interactions, but since none were significant, these were not included in the final models.

At each stage of modelling CAIC was used to recalculate contrasts in order for sample size to be as high as possible. This is necessary since, when calculating multiple contrasts, a species can only be included in the analysis if data are present for all required variables. Missing data cause sample size to decrease rapidly as more variables are included in the analysis.

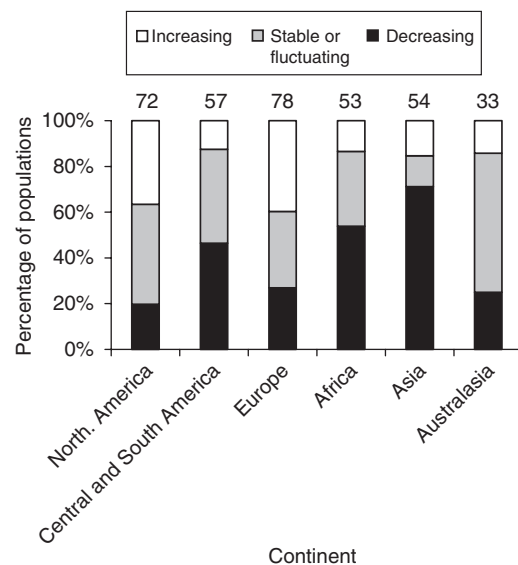
Finally, to test whether intrinsic factors differentially predispose species to being at risk from extrinsic factors, we tested the significance of interaction terms between all intrinsic and extrinsic terms remaining in the MAM.

## Results

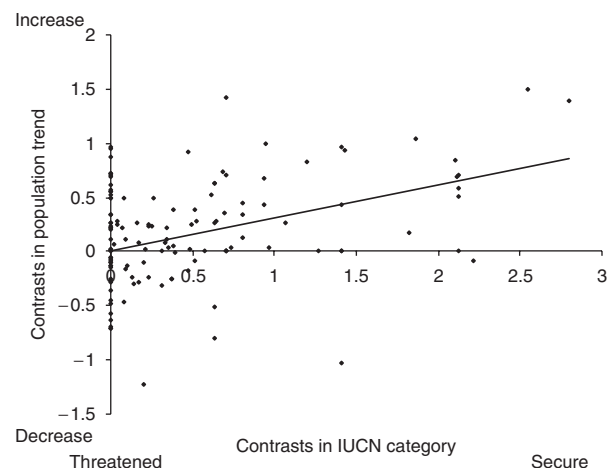
Of 458 populations of 161 Anseriform species, population trends were available for 347 populations. Of these, 10 populations (2.88%) were extinct; 133 populations (38.33%) were decreasing; 121 populations (34.87%) were stable or fluctuating and 83 populations (23.92%) were increasing. The frequency of each trend category was significantly different between continents ( $\chi^2 = 62.625$ , d.f. = 10,  $P < 0.001$ , Fig. 1). There are proportionally fewer declining Anseriform populations in North America, Europe and Australasia than in south and central America, Africa and Asia. Wildfowl species in more threatened IUCN categories have lower population trend categories ( $r = 0.314$ ,  $P < 0.001$ ,  $n = 129$  contrasts, Fig. 2).

### Intrinsic factors

Species with larger population size and global extent of occurrence have more secure population trends (Fig. 3,

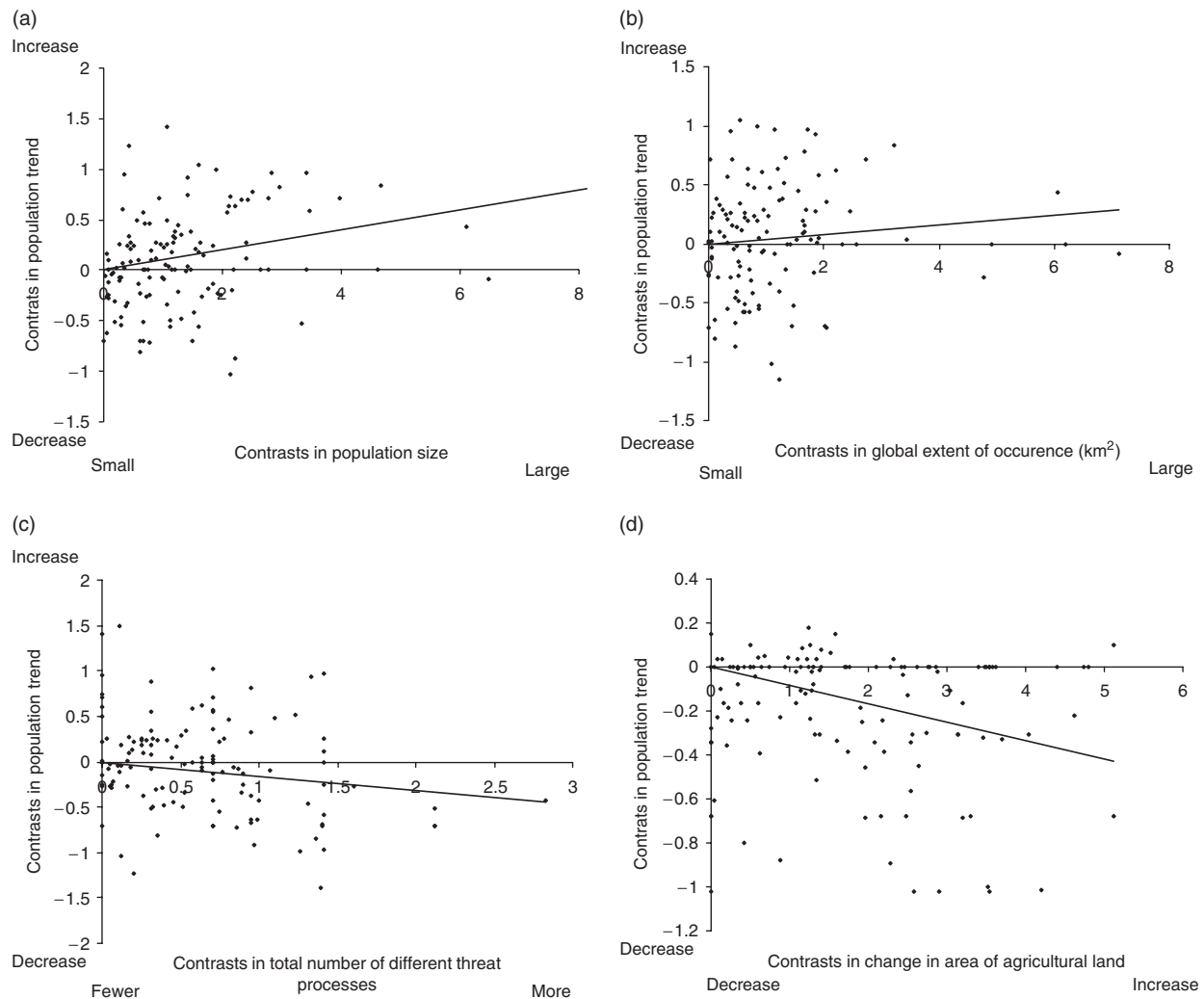


**Figure 1** Frequencies of population trends between continents ( $n = 347$  populations of wildfowl). The number of populations are above each bar.



**Figure 2** Population trend in wildfowl in relation to International Union for the Conservation of Nature (IUCN) category (least squares linear regression through the origin,  $r = 0.134$ ,  $n = 129$  phylogenetically independent contrasts,  $P < 0.001$ ).

population size:  $r = 0.438$ ,  $P < 0.001$ ,  $n = 130$  contrasts; extent of occurrence:  $r = 0.295$ ,  $P < 0.001$ ,  $n = 121$  contrasts). Neither migratory habit ( $r = 0.159$ ,  $P = 0.069$ ,  $n = 130$  contrasts) nor habitat generalism ( $r = 0.112$ ,  $P = 0.201$ ,  $n = 130$  contrasts) related to population trends. Furthermore, trophic levels ( $r = 0.025$ ,  $P = 0.777$ ,  $n = 129$  contrasts), adult body mass ( $r = 0.079$ ,  $P = 0.375$ ,  $n = 126$  contrasts) and fecundity ( $r = 0.227$ ,  $P = 0.264$ ,  $n = 107$  contrasts) are not correlated with population trends. However, larger relative testes are correlated with decreasing populations ( $r = -0.510$ ,  $P = 0.005$ ,  $n = 37$  contrasts) when body mass of males was corrected for.



**Figure 3** Population trend in wildfowl in relation to (a) population size, (b) global extent of occurrence (c) the number of different threat processes, and (d) change in area of agricultural land. See Table 1 for statistics. Bivariate linear regressions through the origin using phylogenetically independent contrasts.

### Extrinsic factors

Neither change in human population density nor per capita water consumption was related to wildfowl population trends (HPD:  $r = -0.001$ ,  $P = 0.315$ ,  $n = 129$  contrasts; water consumption:  $r = 0.000$ ,  $P = 0.673$ ,  $n = 129$  contrasts). However, increase in the area of agricultural land in a species' range is correlated with decreasing population trend ( $r = -0.402$ ,  $P = 0.001$ ,  $n = 129$  contrasts).

A greater number of individual threat processes correlated with decreasing population trend ( $r = -0.160$ ,  $P = 0.004$ ,  $n = 129$  contrasts, Fig. 3). In bivariate analyses, habitat loss/destruction ( $r = -0.255$ ,  $P = 0.030$ ,  $n = 129$  contrasts), pollution ( $r = -0.530$ ,  $P = 0.001$ ,  $n = 129$  contrasts) and invasive species ( $r = -0.477$ ,  $P = 0.044$ ,  $n = 129$  contrasts) were significant predictors of a declining population. Hunting did not predict population trend ( $r = -0.073$ ,  $P = 0.526$ ,  $n = 129$  contrasts), nor did human disturbance

( $r = 0.245$ ,  $P = 0.430$ ,  $n = 129$  contrasts), or accidental mortality ( $r = 0.061$ ,  $P = 0.860$ ,  $n = 129$  contrasts).

We used the test statistics from the bivariate analyses, to test whether intrinsic or extrinsic factors predict better population declines. We compared the absolute values of  $r$  (Table 1) between bivariate analyses of population trend with intrinsic and extrinsic explanatory variables. The predictive power of intrinsic and extrinsic variables, however, was not different (two-sample  $t$ -test,  $t_{16} = 0.221$ ,  $P = 0.828$ ).

### Multiple regressions

The minimum adequate model retained population size, global extent of occurrence, number of different threat processes and change in area of agricultural land as explanatory variables (Table 2). Population size, occurrence and change in area of agricultural land remained highly significant in the model, whereas the number of different process



**Table 1** Population trend (response variable) in relation to intrinsic and extrinsic threats in wildfowl using phylogenetically independent contrasts (bivariate least squares linear regressions through the origin)

Hypotheses	Explanatory variables	<i>r</i>	No. of contrasts	<i>P</i>
Intrinsic				
Population/range	Population size	0.438	130	<0.001
	Global extent of occurrence	0.295	121	0.001
Ecological	Migration	0.159	130	0.069
	Habitat generalism	0.027	129	0.522
	Trophic level	0.025	129	0.777
	Latitude	-0.153	129	0.257
Life-history	Adult mass	0.079	126	0.375
	Fecundity	0.045	126	0.264
Sexual selection	Testes mass <sup>a</sup>	-0.510	37	0.005
Extrinsic				
Threat processes	Number of different threat processes	-0.160	129	0.004
	Habitat loss/destruction	-0.255	129	0.030
	Hunting	-0.073	129	0.526
	Pollution	-0.530	129	0.001
	Invasive species	-0.477	129	0.044
	Human disturbance	0.245	129	0.430
	Accidental mortality	0.061	129	0.860
	Change in human population density	-0.001	129	0.315
Human impact	Water consumption/capita	0.000	129	0.673
	Change in area of agricultural land	-0.402	129	0.001

<sup>a</sup>Male body mass was also included as an explanatory variable.

**Table 2** Minimum adequate model of population trend of wildfowl using phylogenetically independent contrasts

Response variable	Explanatory variables	<i>B</i>	<i>t</i>	<i>P</i>
Population trend	Population size	0.092	2.851	0.0052
	Global extent of occurrence	0.084	2.916	0.0013
	Number of different threat processes	-0.140	-2.112	0.0421
	Change in area of agricultural land	-0.212	-2.259	0.0063

Full model:  $r^2 = 0.312$ ,  $F_{4,129} = 8.178$ ,  $P < 0.001$ .

Excluded variables: habitat loss, pollution, invasive species.

Slope (*B*), *t*-test statistic (*t*) and probability of *t*-test statistic (*P*) are given.

was less so (Table 2). The first-order interactions between intrinsic and extrinsic variables were not significant, so these were eliminated during the process of modelling.

## Discussion

Our analyses suggest that both intrinsic and extrinsic factors predict population trends. While the MAM has moderate predictive power ( $r^2 = 0.312$ ) this is quite impressive given the geographically broad scale of study and relatively crude variables represented by scores. The most strongly supported general hypothesis was that a larger population size and range predispose a species to more secure population trend. In the MAM, global extent of occurrence emerged as a stronger predictor of conservation population trend than population size. This contradicts the conclusion of Gaston & Blackburn (1996) who considered that geographic range was less important than the size of the population within that range. Our results suggest that population size and range are closely related, but also that the area of suitable

habitat within a species' range – the area of occupancy – may be a better predictor, since it integrates the two measures.

Green (1996) found that non-migratory wildfowl were in significantly more threatened IUCN categories. He suggests that this result is due to the large number of threatened non-migratory island endemic wildfowl and also argues that the majority of migratory flyways occur at high latitudes in the northern hemisphere where human impacts on wetland habitats are relatively less adverse than at more equatorial latitudes where greater numbers of non-migratory species are found. In our study we found no relationship between migration and population trend. An important difference between our study and Green (1996) is that we carried out the analyses using phylogenetic correction using 130 species for the tests of the migration hypothesis, whereas Green analysed 235 taxa, many of which are non-migratory island sub-species. Thus phylogenetic non-independence of populations (such as in closely related non-migratory *Anas* species that breed on islands) may have biased his results.

Relative testes mass, a *proxy* for the intensity of sperm competition, was significantly correlated with decreasing population trend. This is consistent with the results of Morrow & Pitcher (2003) and Thomas, Lanctot & Szekely (2006), and support the hypothesis that sexual competition may influence population viability in highly sexually selected species. Note however, that due to the small sample sizes, testes mass was not included in the multiple regression models.

An increase in human population density does not directly predict decreasing populations. This may be due to human environmental impacts, such as pollution and hunting, on wetland birds being lesser in more industrialized states. It could also be possible that the most serious habitat modifications took place in the past and that the wildfowl populations observed today have experienced an extinction filter (Balmford, 1996). Interestingly, water consumption per capita does not perform well as a predictor of population trend in Anseriformes. This may be because high water use does not necessarily imply high demands on natural wetlands.

The most important extrinsic factors retained in the MAM were the total number of threat processes and the change in area of agricultural land. It is important that both add explanatory power beyond that provided by either population size and geographic range size. This suggests that these external factors may be used to identify regions where wetlands are expected to be increasingly threatened in future. We believe that changes in the area of agricultural land are reflecting destruction or degradation of some types of wetland habitats such as drainage of marshes and shallow lakes which in turn have significant effects on wildfowl populations. That the total number of threat processes is significant, suggests that human threats, which individually do not seriously affect a species, may act synergistically to reduce fitness.

Although in bivariate analyses there was no significant overall difference in the variation in population trend explained by intrinsic and extrinsic factors, our analyses may not have identified other important extrinsic factors driving wildfowl declines. McKinney (2001) argued that the relationship between human population density, anthropogenic habitat modification and animal population decline is complex and may vary geographically and affect different taxonomic groups in different ways. Further research, of extrinsic factors more directly linked to wildfowl populations, such as rates of wetland habitat loss, at multiple spatial scales is needed to address this issue.

Taken together, our results suggest that both intrinsic and extrinsic variables predict the conservation status of wildfowl and that measures of population size and range perform best. Attempts to model conservation status using data on extrinsic threats from human activities are challenging given the complex nature of the interactions and the difficulty of selecting appropriate measures of human impact.

There is great diversity in the proportions of threatened species across bird families. Some families such as Psittacidae and Phasianidae contain substantially more threatened

taxa than may be expected by chance and some such as Picidae contain substantially fewer (Bennett & Owens, 1997). Anatidae and Anhimidae are intermediate families in terms of overall levels of threat.

This study of Anseriformes has allowed us to collate a high-quality dataset to explore in detail the factors affecting extinction risk across a whole global bird order, an approach recommended by Fisher & Owens (2004). The most important intrinsic factors driving declines in wildfowl, population size and range size, have been reported as responsible for declines in other bird groups (Blackburn & Gaston, 2002). However, we believe that the extrinsic factors contributing to declines operate in an idiosyncratic way in different groups. For example, anthropogenic impacts on wetlands are unlikely to affect groups in which forest birds predominate. Further studies exploring how anthropogenic factors operate differently across taxonomic groups, ecological guilds and in different geographical regions would be extremely valuable and have the potential to make great contributions to informing conservation priorities.

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## References

- Arnold, K.E. & Owens, I.P.F. (2002). Extra-pair paternity and egg dumping in birds: life-history, parental care and the risk of rehabilitation. *Proc. Roy. Soc. Lond. Ser. B* **269**, 1263–1269.
- Balmford, A. (1996). Extinction filters and current resilience: the significance of past selection pressures for conservation biology. *Trends Ecol. Evol.* **11**, 193–196.
- Bennett, P.M. & Owens, I.P.F. (1997). Variation in extinction risk among birds: chance or evolutionary predisposition? *Proc. Roy. Soc. Lond. Ser. B* **264**, 401–408.
- BirdLife International. (2004). *Threatened birds of the world*. Cambridge, UK: BirdLife International, CD-ROM.
- Blackburn, T.M. & Gaston, K.J. (2002). Extrinsic factors and the population sizes of threatened birds. *Ecol. Lett.* **5**, 568–576.
- Blomberg, S.P., Garland, T. & Ives, A.R. (2003). Testing for phylogenetic signal in comparative data: behavioural traits are more labile. *Evolution* **57**, 717–745.
- Briskie, J.V. & Mackintosh, M. (2004). Hatching failure increases with severity of population bottlenecks in birds. *Proc. Natl. Acad. Sci. USA* **101**, 558–561.
- Brown, L.H., Urban, E.K. & Newman, K. (1982). *Birds of Africa*. Vol. 1. Orlando, UK: Academic Press.

- Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multi-model inference: a practical information-theoretic approach*. 2nd edn. New York: Springer-Verlag.
- Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J.L., Bielby, J. & Mace, G.M. (2004). Human population density and extinction risk in the world's carnivores. *PLoS Biol.* **2**, 909–914.
- Cramp, S. & Simmons, K.E.L. (1984). *Birds of the Western Palearctic. Vol. 1: Ostrich to Ducks*. Oxford, UK: Oxford University Press.
- Del Hoyo, J., Elliot, A. & Sargatal, J. (1992). *Handbook of birds of the world*. Barcelona: Birdlife International/Lynx Edicions.
- Diamond, J.M. (1984). 'Normal' extinctions of isolated populations. In *Extinctions*: 191–246. Nitecki, M.H. (Ed.). Chicago: Chicago University Press.
- Duncan, R.P., Blackburn, T.M. & Worthy, T.H. (2002). Prehistoric bird extinctions and human hunting. *Proc. Roy. Soc. Lond. Ser. B* **269**, 517–521.
- Dunn, P.O., Whittingham, L.A. & Pitcher, T.O. (2001). Mating systems, sperm competition and the evolution of sexual dimorphism in birds. *Evolution* **55**, 161–175.
- Felsenstein, J. (1985). Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15.
- Figuerola, J. & Green, A.J. (2000). The evolution of sexual dimorphism in relation to mating patterns, cavity nesting, insularity and sympatry in the Anseriformes. *Funct. Ecol.* **14**, 701–710.
- Fisher, D.O. & Owens, I.P.F. (2004). The comparative method in conservation biology. *Trends Ecol. Evol.* **19**, 391–398.
- Food and Agriculture Organisation of the United Nations. (2005). <http://faostat.fao.org> accessed 10/08/05
- Freckleton, R.P., Harvey, P.H. & Pagel, M. (2002). Phylogenetic analysis and comparative data: a test and review of the evidence. *Am. Nat.* **160**, 712–726.
- Furness, R.W. & Greenwood, J.J.D. (Eds) (1993). *Birds as monitors of environmental change*. London: Chapman & Hall.
- Gage, G.S., Brooke, M.L., Symonds, M.R.E. & Wege, D. (2004). Ecological correlates of the threat of extinction in Neotropical bird species. *Anim. Conserv.* **7**, 161–168.
- Garland, T., Harvey, P.H. & Ives, A.R. (1992). Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* **41**, 18–32.
- Gaston, K.J. (1994). *Rarity*. London: Chapman & Hall.
- Gaston, K.J. & Blackburn, T.M. (1995). Birds, body size and the threat of extinction. *Phil. Trans. Roy. Soc. Lond. Ser. B* **347**, 205–212.
- Gaston, K.J. & Blackburn, T.M. (1996). Global scale macroecology: interactions between population size, geographic range and body size in the Anseriformes. *J. Anim. Ecol.* **65**, 701–714.
- Gleick, P.H. (1998). *The world's water 1998–1999*. Washington, DC: Island Press.
- Green, A.J. (1996). Analyses of globally threatened Anatidae in relation to threats, distribution, migration patterns and habitat use. *Conserv. Biol.* **10**, 1435–1445.
- Harvey, P.H. & Pagel, M.D. (1991). *The comparative method in evolutionary biology Oxford Series in Ecology and Evolution*. Oxford: Oxford University Press.
- Ihaka, R. & Gentleman, R. (1996). R: a language for data analysis and graphics. *J. Comput. Graph. Stat.* **5**, 299–314.
- IUCN. (2001). *International union for the conservation of nature Red List categories. Version 3.1*. Gland, Switzerland: IUCN.
- Kokko, H. & Brooks, R. (2003). Sexy to die for? sexual selection and the risk of extinction. *Ann. Zool. Fenn.* **40**, 207–219.
- Kunin, W.E. & Gaston, K.J. (1997). *The biology of rarity*. London: Chapman & Hall.
- Liu, J., Daily, G.C., Ehrlich, P.R. & Luck, G.W. (2003). Effects of household dynamics on resource consumption and biodiversity. *Nature* **421**, 530–533.
- Livezey, B.C. (1986). A phylogenetic analysis of recent Anseriform genera using morphological characters. *Auk* **103**, 737–754.
- Mace, G.M. & Stuart, S. (1994). IUCN Red List categories. *Species* **21–22**, 13–24.
- Marchant, S. & Higgins, P.J. (1990). *Australian, New Zealand and Antarctic birds. Vol. 1. Australian pelicans to ducks*. Melbourne: Oxford University Press.
- McKinney, M.L. (2001). Role of human population size in raising bird and mammal threat among nations. *Anim. Conserv.* **4**, 45–57.
- Moller, A.P. (2000). Sexual selection and conservation. In *Behaviour and conservation*: 55–60. Gosling, M.L. & Sutherland, W.J. (Eds). London: Academic Press.
- Monroe, B.L. & Sibley, C.J. (1993). *A world checklist of birds*. Yale: Yale University Press.
- Morrow, E.H. & Pitcher, T.E. (2003). Sexual selection and the risk of extinction in birds. *Proc. Roy. Soc. Lond. Ser. B* **270**, 1793–1799.
- Moser, M., Prentice, C. & Frazier S. (1996). A global overview of wetlands loss and degradation. In *Technical session B of the RAMSAR Conference of Parties (COP)*: 21–31. New York & Brisbane: UNFCCC.
- Pimm, S.L., Jones, H.L. & Diamond, J. (1988). On the risk of extinction. *Am. Nat.* **132**, 757–785.
- Poole, A. & Gill, F. (1995). *The birds of North America*. Philadelphia: The Academy of Natural Sciences, and The American Ornithologists' Union.
- Purvis, A. & Rambaut, A. (1995). Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Comp. Appl. Biosci.* **11**, 247–251.
- Simberloff, D. (1998). Small and declining populations. In *Conservation science and action*: 116–134. Sutherland, W.J. (Ed.). Oxford, UK: Blackwell Science.

- Stevens, G.C. (1989). The latitudinal gradient in geographical range: How so many species coexist in the tropics. *Am. Nat.* **133**, 240–256.
- Thomas, G.H., Lanctot, R.B. & Szekely, T. (2006). Can intrinsic factors explain population declines in North American shorebirds? A comparative analysis. *Animal Conservation* **9**, 252–258.
- Todd, F.S. (1996). *Natural history of the waterfowl*. Vista, CA: San Diego Natural History Museum. Ibis Publishing.
- United Nations Population Division (2004). *World population prospects: the 2004 revision*. [http://www.un.org/esa/population/publications/WPP2004/2004Highlights\\_finalrevised.pdf](http://www.un.org/esa/population/publications/WPP2004/2004Highlights_finalrevised.pdf) (accessed on 12/07/05).
- Wetlands International. (2002). *Waterbird population estimates. Wetlands international global series no. 12*. 3rd edn. Wageningen, the Netherlands: Wetlands International.

## **Chapter 4** Why are wetland birds declining globally?

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### **Manuscript**

#### **Details and extent of the contributions by authors**

**P.R. Long:** data collection, statistical analysis, manuscript writing (75%)

**M.J. O'Connell:** general editing of the manuscript, suggestions to improve the study (5%)

**B. Hughes:** suggestions to improve the study (5%)

**S. Delany:** data provision, suggestions to improve the study (5%)

**T. Székely:** general editing of the manuscript, suggestions to improve the study (10%)

## **Abstract**

In this study we explore the factors associated with decreasing and increasing population trends in all wetland birds, a globally distributed ecological group of birds. To better understand the mechanisms threatening wetland birds, we modelled population trends among all species of wetland birds in relation to population size, global range, mean adult mass, latitude of the breeding range and human population density in the breeding range and then compared each of twenty three taxonomic groups of wetland birds with our overall model to identify groups of birds which are threatened in idiosyncratic ways. There are proportionally more declining rail, snipe and sandpiper species and proportionally fewer declining swans, pelicans and gulls. Overall, species with larger mean adult mass and larger population size have more secure population trends and there is no overall association between population trend and either latitude or human population density. However these patterns are not consistent across taxonomic groups: species in some groups are more resilient to a particular threat than species in other groups which are more susceptible. We discuss the implications of these patterns for estimation of latent extinction risks used to inform species prioritisation.

## INTRODUCTION

At a global scale, wetland ecosystems are significantly threatened by human impacts. Since wetlands are highly productive ecosystems, often found on flat terrain and in coastal regions, they have been susceptible to these human impacts for centuries. It is important to monitor the biodiversity of wetlands, not least because wetland species can act as indicators of the integrity of the system and the ecosystem services that a wetland provides. In order to effectively conserve wetland ecosystems, it is essential to understand the drivers of species using these habitats.

Wetland bird population declines may be driven by a variety of processes. First, a species' population size may be an important predictor of population trend because demographic, genetic and environmental stochasticity and catastrophes, are relatively more important in small populations than larger populations (Simberloff 1998). Demographic stochasticity, however, is thought to be relatively unimportant in populations larger than roughly 1000 individuals (Lande 1993).

Second, life-history strategy may play an important role in determining the susceptibility of a species to environmental perturbation. We use adult body mass as a *proxy* measure of life-history since body mass in birds is strongly correlated with annual survival, fecundity and clutch size (Bennett & Owens 2002). Large body size is associated with a more K-selected life history, in which the rate of population growth is limited by fecundity and the constraints imposed by the environment. As such, larger wetland birds may be more predisposed to declines as they are less able to vary their rate of population growth (Gaston & Blackburn 1995).

Among all globally threatened birds, 1008 (85%) are threatened by habitat loss and degradation, making this the leading single cause of endangerment in birds (Birdlife International 2000).

Human population density (HPD) in the breeding range can be used as a *proxy* for all human impacts such as habitat modification, invasive species, pollution and hunting on wetland environments within the breeding range of a species. We might expect that species with greater HPD in their breeding range have more declining population trends than species which co-exist with fewer people.

Finally, we also expect that high HPD may interact with body size such that larger species will be more threatened for a given level of human impact than smaller species since larger, more K-selected, species may be less able to adapt to anthropogenic pressures such as hunting or extensive habitat modification (Bennett & Owens 2002).

In this study we explore the factors associated with decreasing and increasing population trends in a globally distributed ecological group of birds. We use population trend as our response variable as this may be observed objectively and is independent of any prioritisation procedure. We are interested in understanding threats to wetland birds in general, but recognise that there may be non-uniform responses among different taxonomic groups. We therefore also test our hypotheses in twenty three taxonomic groups recognised by Monroe & Sibley (1993) and compare each group with the overall model.

Wetland birds are excellent organisms to test conservation biological hypotheses. First, wetland birds are a highly diverse, globally distributed ecological group. For instance, they live on all continents (except Antarctica), and have a good range of life history traits, as reflected by differences in body size across three orders of magnitude. Second, excellent monitoring data has been systematically collected globally since 1994 (Rose & Scott 1994). They are also recognised to be particularly good indicator species for the integrity of wetlands (Furness & Greenwood 1993).

## **METHODS**

We collected data from Waterbird population estimates fourth edition (WPE; Wetlands International 2006) on size and trend of 2239 populations of 865 species of wetland birds recognised as species by Monroe & Sibley (1993).

### *Species data*

Population trend was represented by 1 = Extinct, 2 = Declining, 3 = Stable, 4 = Increasing (Wetlands International 2006). For those species that had more than one population of known population trend, we calculated a median population trend.



For each species, all population sizes reported in WPE were summed to obtain a total global population size. Global extents of occurrence (in km<sup>2</sup>) were obtained from Threatened Birds of the World (TBW, BirdLife International 2004). Population sizes and range sizes were log transformed prior to analysis.

Adult male mass (in grams) and adult female mass (in grams) were used to calculate a mean adult mass. Adult mass was log transformed before analysis.

We used shapefiles describing the global breeding ranges of all wetland bird species (Orme *et al.* 2005) to calculate median human population density (Dobson 2000) within each species' breeding range using zonal statistics in ArcGIS 9.0. Using the same species range shapefiles, we also calculated the co-ordinates of the centroid of each polygon, and recorded the latitude in decimal degrees. We then took the absolute value of the latitude in order to measure distance from the equator either to the north or south and log-transformed this value prior to analysis.

### *Models*

We first used five bivariate least squares linear regressions to model the relationship between population trend and adult mass, population size, latitude, HPD and the interaction adult mass:HPD at the species level for all wetland birds. Second, we constructed a full multiple model using all explanatory variables which were significant ( $p < 0.05$ ) in bivariate models and their first-order interactions. To reach the minimum adequate model (MAM) we then successively removed terms from the full model until all remaining terms were significant. We conducted this modelling procedure at species level, taking no account of phylogenetic non-intdependence. Since neither a composite tree or supertree exists for our set of species we did not have a phylogenetic hypothesis to use as the basis for a phylogenetic generalised linear model (PGLM).

Finally, we repeated the five bivariate least squares linear regressions for population trend with respect to adult mass, population size, latitude, HPD and the interaction adult mass:HPD for each of 23 taxonomic groups of wetland birds. This allowed us to estimate an  $r$  value and standard

error for each model for comparison with the appropriate parameter estimates from the models relating to all wetland birds in order to see which groups conform with the overall patterns for all wetland birds and which exhibit significantly different relationships.

## RESULTS

### *Distribution of population trends*

Of 835 species of wetland birds, 600 species had a known trend for at least one population. Of these, 20 species (3.33%) were extinct; 229 species (38.17%) were decreasing; 282 species (47.00%) were stable and 69 species (11.50%) were increasing. The frequency of species in each trend category was significantly different between groups of wetland birds ( $\chi^2 = 143.09$ , d.f. = 66,  $p < 0.001$ , Fig. 1). There are proportionally more declining rail, snipe and sandpiper species and proportionally fewer declining swans, pelicans and gulls.

### *All wetland birds*

Among all wetland birds, species with larger mean adult mass and larger population size have more secure population trends (Table 1, Fig. 2, adult mass:  $r = 0.085$ ,  $p < 0.001$ ,  $n = 542$  species; population size:  $r = 0.062$ ,  $p < 0.001$ ,  $n = 544$  species). Overall, there was no association between latitude of the centroid of the breeding range, HPD in the breeding range or the interaction adult mass : HPD and population trend (Table 1, latitude:  $r = 0.034$ ,  $p = 0.159$ ,  $n = 568$  species; HPD:  $r = -0.019$ ,  $p = 0.105$ ,  $n = 565$  species; adult mass : HPD:  $r = 0.000$ ,  $p = 0.840$ ,  $n = 522$  species). The relationship between HPD and population trend is close to marginal significance ( $p < 0.1$ ) suggesting that species with lower HPD in their breeding range may be less threatened.

The minimum adequate model for all wetland birds retained adult mass and population size as explanatory variables (Table 2). We also tested the first-order interaction between adult mass and population size, but this was not significant and so was eliminated.

**Table 1.** Population trend (response variable) in relation to predictors of threat in wetland birds. Bivariate least squares linear regression.

Response variable	Explanatory variable	r	n (species)	p
Population trend	Adult mass	0.085	542	<0.001
Population trend	Population size	0.062	544	<0.001
Population trend	Latitude	0.034	568	0.159
Population trend	Human population density	-0.019	565	0.105
Population trend	Adult mass : Human population density	0.000	522	0.84

**Table 2.** Minimum adequate model of population trend in wetland birds.

Response variable	Explanatory variables	$\beta$	t	p
Population trend	Adult mass	0.089	4.481	<0.001
	Population size	0.052	4.849	<0.001
Full model: $R^2 = 0.08$ , $F_{2,504} = 21.05$ , $P < 0.001$				
Excluded variables: Latitude, Human population density, Adult mass : Human population density				
Partial slope ( $\beta$ ), t-test statistic (t) and probability of t-test statistic (p) are given				

#### *Individual taxonomic groups*

When we repeated the bivariate models for each taxonomic group of birds separately we found that the population trend of species in different taxonomic groups appears to respond to potential threat processes differently to the overall model containing all wetland birds (Table 3, Fig. 3).

Among all wetland birds, greater adult mass was associated with increasing population trend. Although stiff-tailed ducks and swans fit with this pattern, the slope of their relationships was significantly greater than the overall model. Ducks, snipe, jacanas, terns, grebes, flamingos and pelicans did not conform with the overall model – in these groups, the larger species have a significantly more declining population trend than in all wetland birds (Table 3, Fig. 4a).

Overall, greater population size is associated with increasing population trend. This effect is especially pronounced in geese, avocets, herons, flamingos, pelicans and storks. In these groups, species with larger population sizes have significantly more increasing population trends than the model for all wetland birds predicts. Conversely, in cranes and oystercatchers species with larger

populations are significantly more threatened than the overall model for all wetland birds (Table 3, Fig 4b).

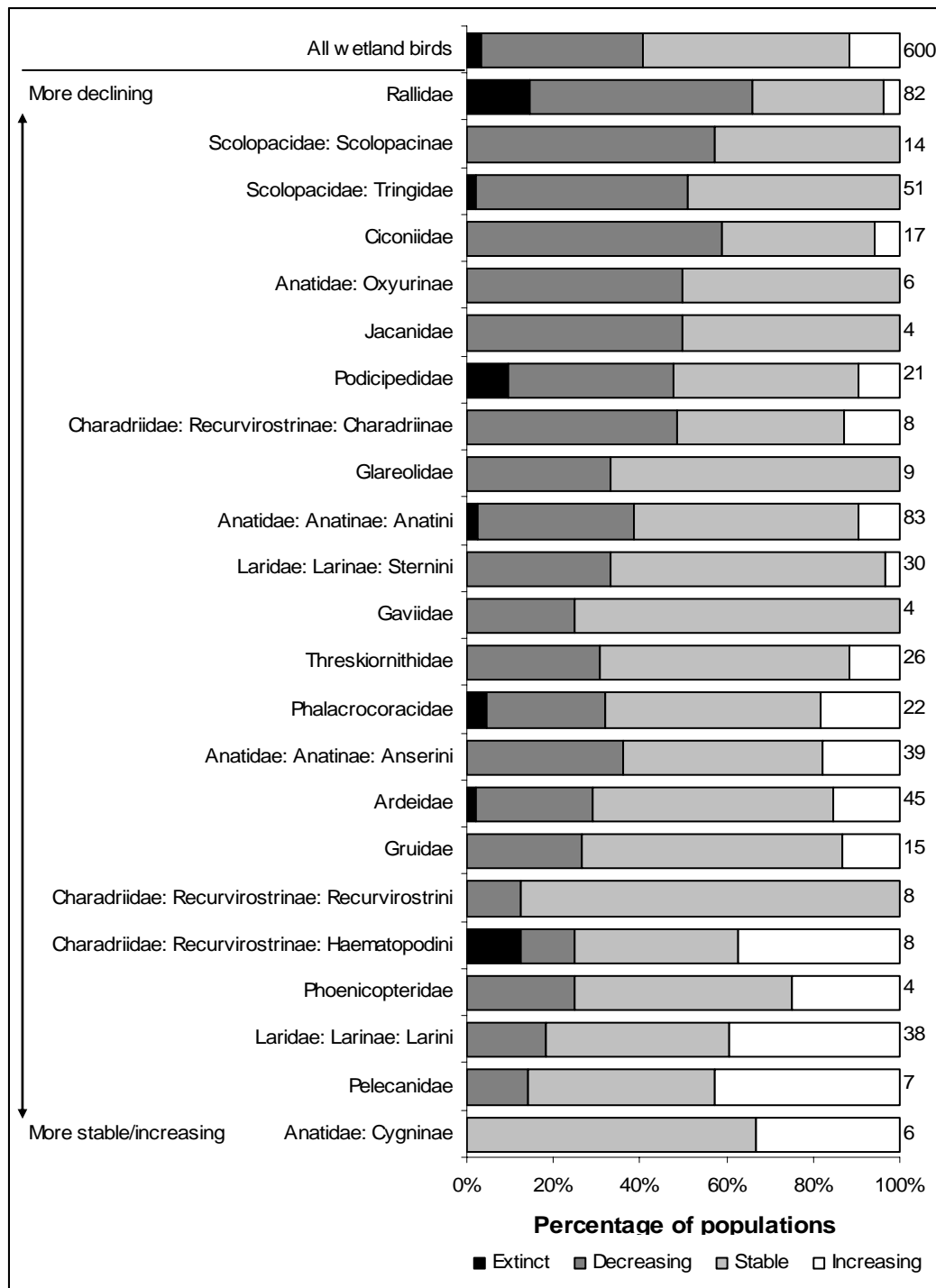
There was no significant association between population trend and the latitude of the centroid of the breeding range in a model considering all wetland birds. However, a pattern was apparent in some groups: stiff-tailed ducks, geese, cranes, rails, snipe and sandpipers are groups in which more equatorial species have more increasing population trends. The opposite effect is seen in jacanas, terns and herons, in which higher latitude breeding species have more increasing population trends (Table 3, Fig 4c).

There was no significant association overall between HPD in the breeding range and population trend. However separate models for each group showed that gull and flamingo species are more likely to have more increasing population trends at higher levels of HPD. In contrast, geese, rails, snipe, pratincoles and storks are groups in which higher levels of HPD are associated with significantly more declining population trend than the null model.

We tested for the effect on population trend of an interaction between adult mass and HPD in the breeding range and found no effect overall. However in flamingos this interaction was significant: larger flamingo species have more increasing population trend at higher levels of HPD (Table 3, Figure 4e).

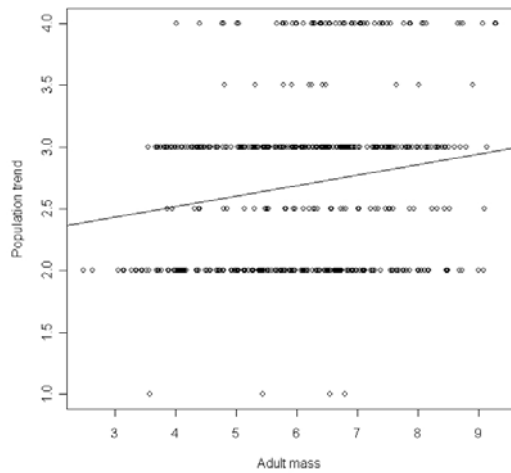
**Table 3.** r values of bivariate least squares linear regressions of population trend in relation to predictors of threat in wetland birds.

Family: Sub-family: Tribe	Adult mass	Population size	Latitude	HPD	Adult mass : HPD
Anatidae: Oxyurinae	-0.839	0.036	0.005	-0.075	-0.023
Anatidae: Cygninae	0.916	0.047	0.002	-0.001	0.002
Anatidae: Anatinae: Anserini	0.125	0.091	0.005	-0.101	-0.013
Anatidae: Anatinae: Anatini	-0.133	0.035	-0.002	0.009	0.001
Gruidae	0.009	-0.079	0.007	-0.009	-0.001
Rallidae	0.060	0.076	0.001	-0.092	-0.007
Scolopacidae: Scolopacinae	-0.482	0.089	0.001	-0.133	-0.027
Scolopacidae: Tringidae	0.058	0.019	0.017	-0.032	-0.008
Jacaniidae	-0.196	0.173	-0.009	-0.162	-0.039
Charadriidae: Recurvirostrinae: Haematopodini	0.124	-0.225	0.007	-0.338	-0.012
Charadriidae: Recurvirostrinae: Recurvirostrini	0.092	0.106	0.004	-0.032	-0.009
Charadriidae: Recurvirostrinae: Charadriinae	0.176	0.044	-0.005	0.012	0.005
Glareolidae	0.106	0.112	-0.004	-0.181	-0.401
Laridae: Larinae: Larini	0.155	0.048	-0.002	0.095	0.017
Laridae: Larinae: Sternini	0.277	0.033	-0.001	-0.011	0.014
Podicipedidae	-0.331	0.068	-0.003	-0.075	-0.017
Phalacrocoracidae	0.129	0.073	-0.002	0.017	0.005
Ardeidae	0.194	0.139	-0.002	-0.047	-0.004
Phoenicopteridae	-0.911	0.263	0.055	0.363	0.047
Threskiornithidae	0.216	0.022	0.000	-0.082	-0.003
Pelecanidae	-0.956	0.127	-0.009	-0.154	-0.021
Ciconiidae	0.276	0.145	-0.006	-0.272	-0.022
Gaviidae	-0.122	0.138	-0.004	-0.127	-0.017
All wetland birds	0.085	0.062	0.002	-0.019	-0.002

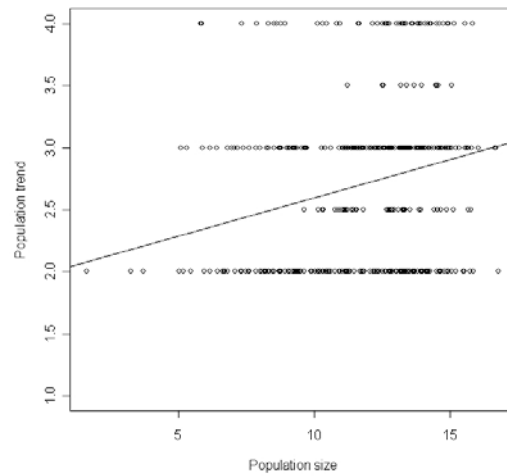


**Figure 1.** Frequencies of species population trends between groups of wetland birds (n = 600 species of wetland birds). The number of species of known trend in each group is shown at the end of each bar. Groups are ordered by mean population trend; from most declining at the top to most stable/increasing at the bottom.

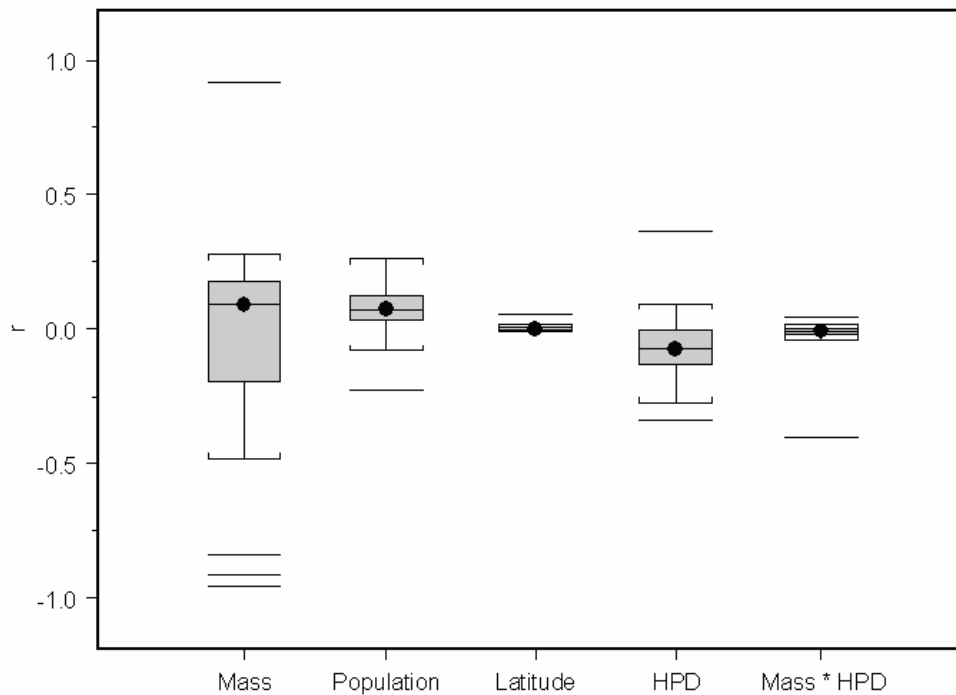
a)



b)



**Figure 2.** Population trend in wetland birds in relation to a) adult mass, b) population size. Least squares linear regression models shown by solid line.



**Figure 3.** Variation in  $r$  values of least squares linear regressions of population trend versus explanatory variable between groups of wetland birds. Median  $r$  values shown by black circles; the grey bars show upper and lower quartiles; whiskers extend to 95% confidence intervals and the floating horizontal lines are outliers.  $n = 23$  groups of wetland birds.

**Figure 4.**  $r$  parameter estimates and standard errors for each group of wetland birds compared to the  $r$  parameter estimate for all wetland birds for the relationship between population trend and a) adult mass, b) population size, c) latitude of centroid of breeding range, d) human population density in breeding range. Bivariate least squares linear regressions. See Table 3 for statistics.

a)

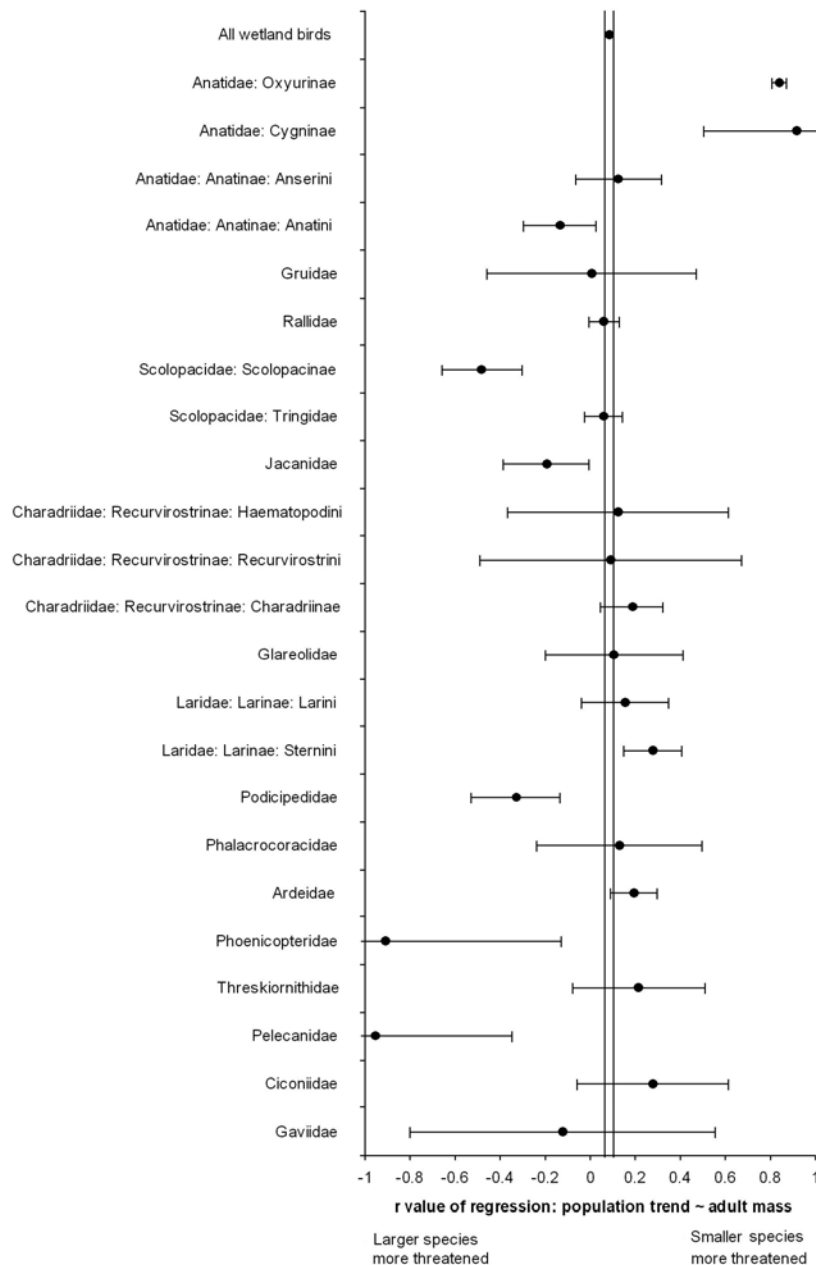




Figure 4. (cont.)  
b)

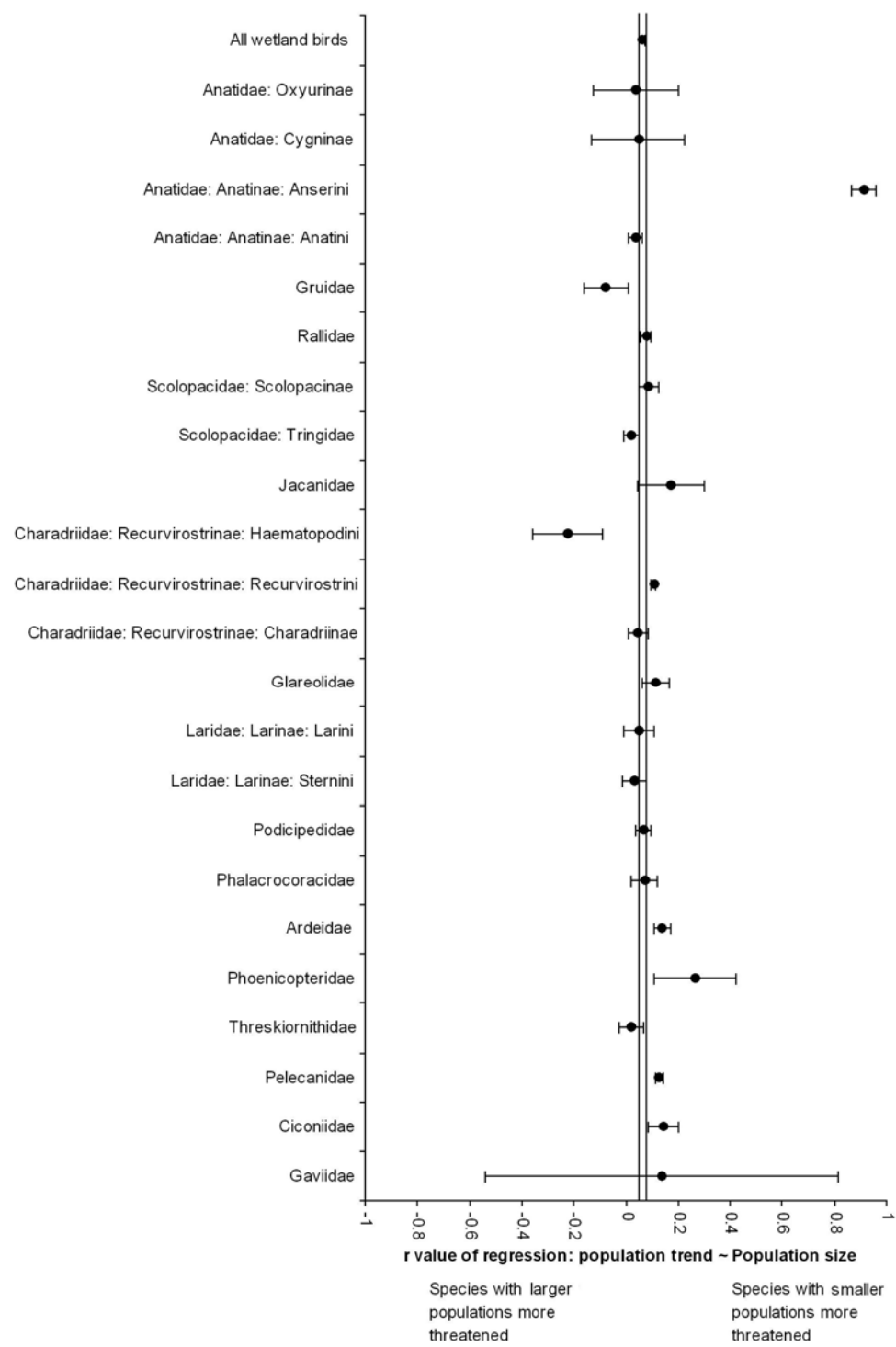


Figure 4. (cont.)  
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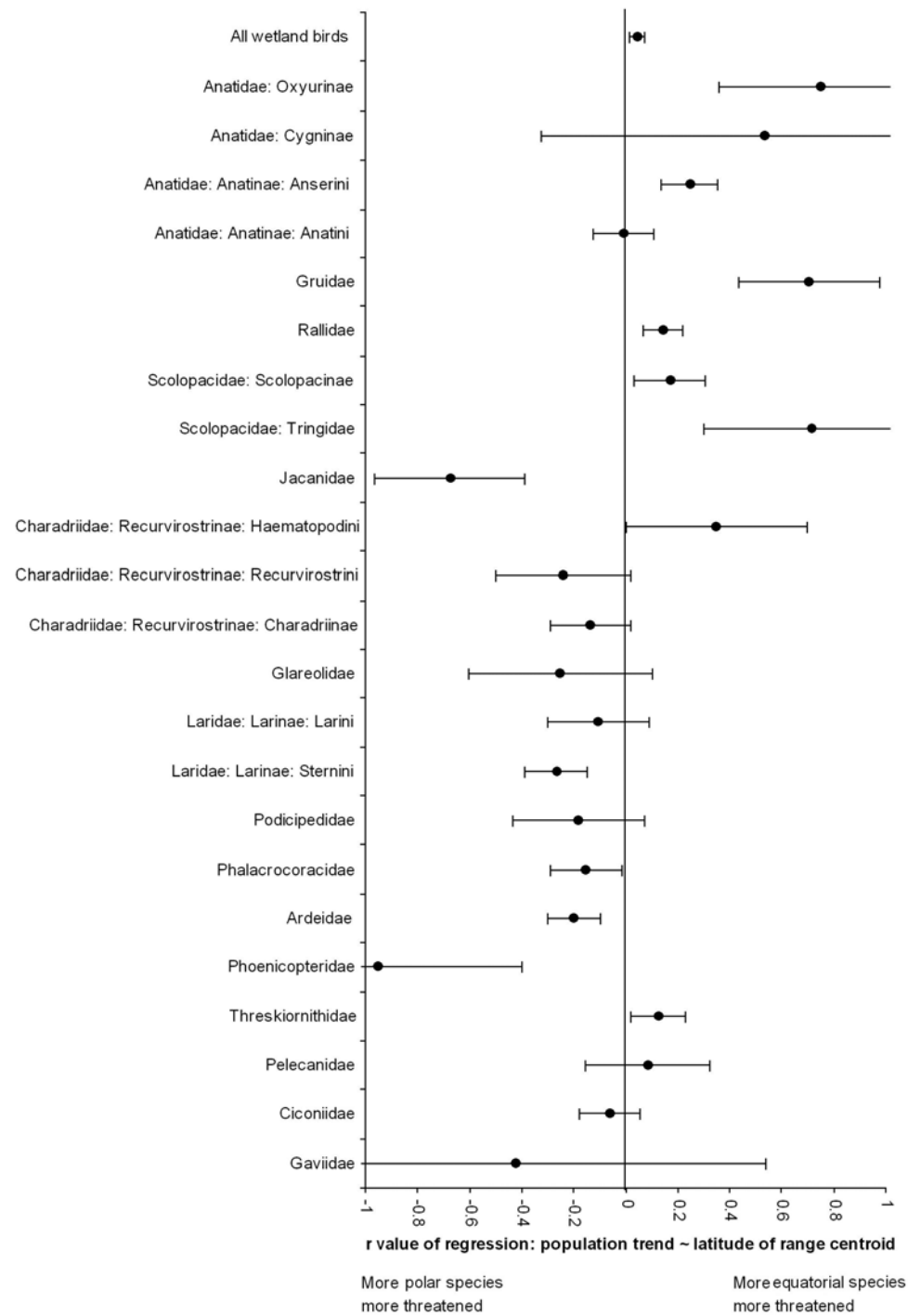


Figure 4 (cont.)  
d)

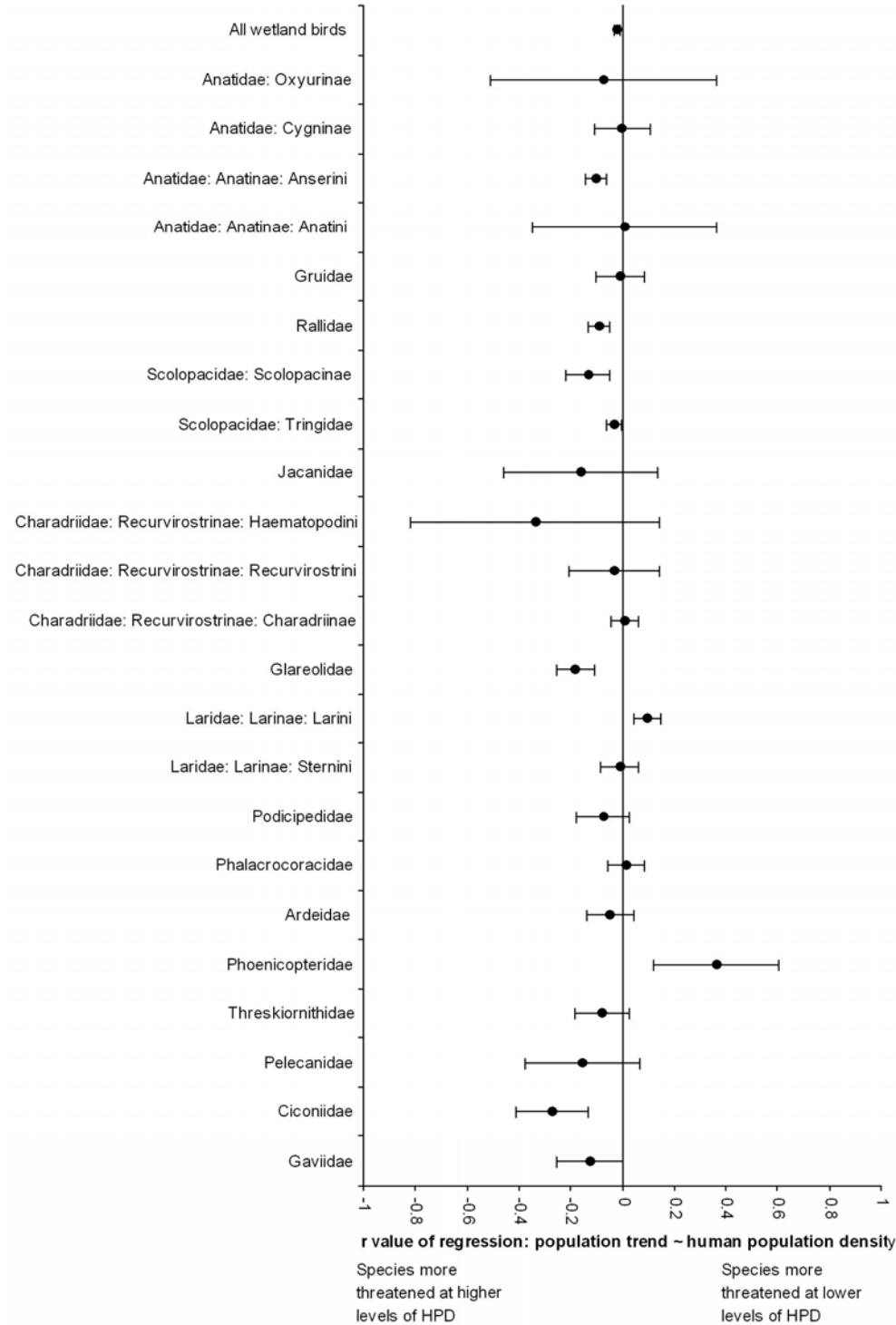
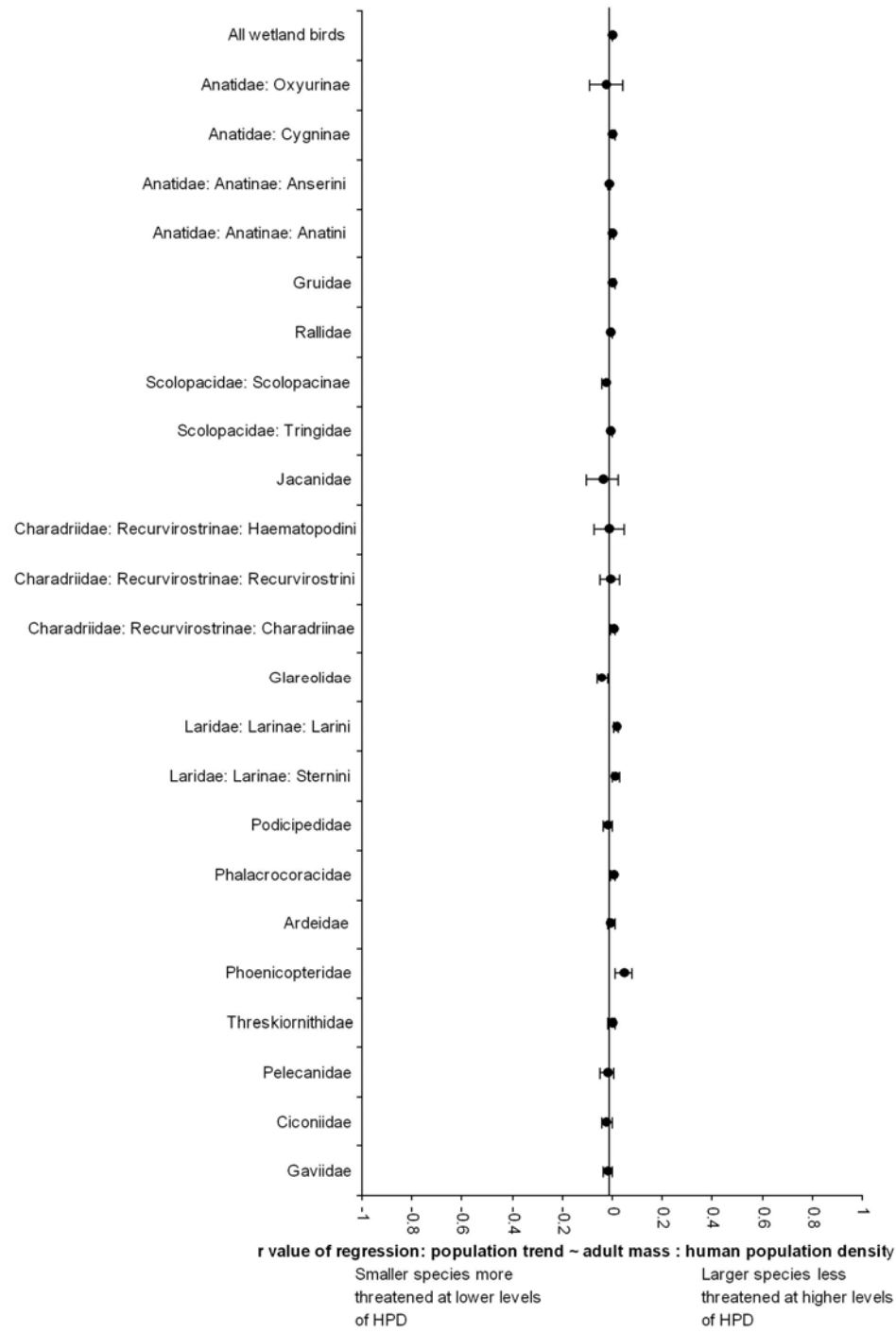


Figure 4 (cont.)  
e)



## DISCUSSION

Our analysis supported the general hypothesis that greater population size is associated with more increasing population trend and we found that, among all wetland birds, larger species also have more secure population trends although the MAM for population trend in all wetland birds had very weak predictive power ( $r^2 = 0.08$ , Table 2). The population size effect is consistent with our hypothesis that small population processes that may predispose a species to decline are do not occur in larger populations. The overall effect of large body is does not accord with the hypothesis that species with a more K-selected life-history may be more likely to decline. However it is possible that an extinction filter effect (Balmford 2000) has operated to produce this overall pattern. There was no overall relationship between population trend and latitude and, across all wetland birds, higher HPD was not associated with declining populations as hypothesised.

Overall, species with smaller body mass have more declining population trends. This is not consistent with the hypothesis that more K-selected species may be more threatened since they are less able to increase fecundity to compensate for mortality in the population. This relationship may be largely driven by rails, a speciose and highly threatened group of relatively small birds. In prehistoric times, as many as 2000 rail species may have become extinct on Pacific islands (Steadman 1995). However, ducks, snipe, jacanas, terns, grebes, flamingos and pelicans have regression slopes significantly less than the overall model, which are consistent with the standard explanation.

It may be that factors such as habitat specialisation are more important for most wetland birds than life-history and that smaller species which typically have more specialised habitat requirements are more threatened as a result of anthropogenic loss and degradation of wetlands rather than through a life-history mechanism. This is especially likely to be the case in stiff-tailed ducks and swans, two groups in which smaller species significantly more threatened than the overall model predicts.

Amongst all wetland birds, species with greater population size have more secure population trends. This effect is especially pronounced in geese, avocets, herons, flamingos, pelicans and storks. In these groups, the regression slopes are significantly greater than the overall model

which suggests that they be especially vulnerable to small population processes. The opposite effect can be seen in cranes and oystercatchers - species with larger populations are significantly more threatened than might be expected given the relationship across all wetland birds.

There was no overall relationship between population trend and latitude. However when groups are compared separately, it appears that jacana, tern, cormorant and heron species breeding further from the equator are currently more threatened. The more polar-breeding species in these groups may be particularly susceptible to climate change at their range margins in future. In the following groups, species breeding nearer the equator are more threatened: stiff-tailed ducks, geese, cranes, rails, snipe and sandpipers. This effect may be due to greater human pressures on wetland birds on oceanic islands, and the effect may also be confounded by Rapoport's rule – equatorial species have smaller ranges (Rapoport 1982).

Although there was no overall association between population trend HPD, the following groups had significantly greater regression slopes than zero, fitting our hypothesis that greater human activity may threaten birds: geese, rails, snipe, pratincoles and storks. However the most threatened gull and flamingo species were those breeding in areas with lower HPD.

Among all wetland birds there was no association between population trend and the interaction between human population density and adult mass. However, larger flamingo species are less threatened at higher HPD (Table 3, Figure 4e). For a given level of human pressures, larger bodied African flamingos are experiencing a greater population decline than smaller Neotropical flamingos. This effect may be exacerbated by the greater coloniality of African flamingos (Reed 1999).

Taken together, our results suggest that wetland birds are threatened for diverse reasons and that there is little consistency in these processes even within the larger families. This finding is important in the context of analyses of latent extinction risk and identification of species which may become more threatened in future (Cardillo et al 2006). It is important in such analyses to understand the correct taxonomic level at which it is possible to generate predictions.

This analysis has allowed us to address potential causes of variation in population trend across a globally distributed ecological group of birds using a high-quality dataset and to explore predictors of declining population trends separately in a number of taxonomic groups. We believe that effective wetland bird conservation first requires that good monitoring data allows declining species to be identified and second, that the causes of declines be understood (Caughley 1994). In this study we show that 23 groups of wetland birds differ in their relative level of threat and also that they have idiosyncratic responses to factors which may predispose them to declining population trends: species in some groups are more resilient to a particular threat than species in another group which are more susceptible. It is essential to incorporate an understanding of this heterogeneity into conservation priority setting, especially with respect to species which are latently threatened.

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### **REFERENCES**

- Bennett , P.M., & Owens, I.P.F. (2002) *Evolutionary ecology of birds: life-histories, mating systems and extinction*. Oxford University Press.
- BirdLife International (2000) *Threatened birds of the world*. Cambridge, UK. BirdLife International.
- Cardillo, M., Mace, G.M., Gittleman, J.L., & Purvis, A. (2006) Latent extinction risk and the future battlegrounds of mammal conservation. *PLOS Biology* 103: 4157-4161

Dobson, J.E., Bright, E.A., Coleman, P.R., Durfee, R.C., & Worley, B.A. (2000) Landscan: a global database for estimating populations at risk. *Photogrammetric Engineering and Remote Sensing* 66: 849-859

Dunning, J.B. (2008) *CRC handbook of avian body masses*. 2<sup>nd</sup> Edition. Boca Raton FL, CRC Press.

Furness, R.W. & Greenwood, J.J.D. (Eds) (1993). Birds as monitors of environmental change. London:Chapman & Hall.

Gaston, K.J. & Blackburn, T.M. (1995). Birds, body size and the threat of extinction. *Philosophical Transactions of the Royal Society of London Series B* 347, 205–212.

Lande, R. (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* 142: 911-927.

Monroe, B.L. & Sibley, C.J. (1993). *A world checklist of birds*. Yale: Yale University Press.

Orme, C.D.M. *et al.* (2005) Global hotspots of species richness are not congruent with endemism or threat. *Nature* 436: 1016-1019

Reed, J.M. (1999) The role of behaviour in recent avian extinctions and endangerments. *Conservation Biology* 13: 232-241

Rapoport, E.H. (1982) *Areography: geographical strategies of species*. Pergamon, Oxford.

Rose, P.M., & Scott, D.A. (1994) *Waterfowl population estimates*. International Waterbirds and Wetlands Research Bureau, Slimbridge, Gloucestershire

Steadman, D.W. (1995) Prehistoric extinctions on Pacific islands: biodiversity meets zooarchaeology. *Science* 247: 1123-1131



Wetlands International (2006) *Waterbird population estimates*. 4<sup>th</sup> edition. Wageningen, The Netherlands, Wetlands International

## **Chapter 5.** Patterns of diversity in European wetland bird communities

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**Manuscript**

### **Details and extent of the contributions by authors**

**P.R. Long:** data collection, statistical analysis, manuscript writing (80%)

**B. Hughes:** suggestions to improve the study (5%)

**T. Székely:** general editing of the manuscript, suggestions to improve the study (5%)

**M.J. O'Connell:** general editing of the manuscript, suggestions to improve the study (10%)

## **Abstract**

Substantial areas of wetlands in Europe have been lost to agriculture and other human land-uses in the past and wetlands remain highly threatened by development today. In this study we explore the patterns of species richness and diversity of birds which are ecologically dependent on wetlands in terms of environmental characteristics of wetlands and measures of human impact in 2012 European Important Bird Areas (IBAs) which contain wetlands. We test the effects of wetland area, habitat diversity, elevation, latitude, isolation from nearest neighbouring wetland and human population density in a buffer surrounding the wetland using Generalised additive models (GAMs) incorporating spatial autocorrelation. Our final models suggest that wetlands with greater species richness are large, at low elevations and in Southern Europe. Wetlands with high species diversity are large, at low elevations and closer to neighbouring wetlands. Taken together, our results suggest that if appropriate measures are taken to conserve and connect wetlands at landscape scale, it is possible for rich and diverse wetland bird communities to coexist with a relatively high density of people in Europe.

## INTRODUCTION

Wetlands in Europe have been extensively modified by human activities over hundreds of years (Hollis & Jones 1991), and these threats continue to the present day. European wetlands are currently threatened by drainage to make land suitable for agriculture, construction of roads and structures such as dykes, levees and sea walls to control flooding, mining of peat, excessive water abstraction, pollution and natural events such as droughts (Dugan 1990; Finlayson et al 1992).

As natural wetlands are modified by human use, patches of remaining habitat become smaller and more isolated (Wiens 1995), and, at a landscape scale, the total area of suitable habitat for wetland dependent plants and animals decreases. A matrix of anthropogenic habitats between suitable patches can potentially reduce the permeability of the landscape to animal movement (Crooks & Sanjayan 2006). Some species are severely threatened by habitat loss and degradation, whereas modified habitats remain acceptable for other species (Brotons et al 2003).

Island biogeography theory was developed to explain the species-area effect, the effect of isolation on species richness and species turnover on islands (MacArthur & Wilson 1967). This body of theory has been extensively tested empirically and has a central role in informing conservation planning at landscape scale and the design of protected areas (Diamond 1976).

The effects of loss and fragmentation of forest habitats on bird communities globally has been well studied, but there have been relatively few studies on the causes of patterns of diversity in wetlands (Brown & Dinsmore 1986, Findlay & Houlihan 1997; Riffell et al 2001; Guadagnin & Maltchik 2007).

In this study we explore the patterns of species richness and diversity of European birds which are ecologically dependent on wetlands. Since wetland birds are dependent on

wetlands, a naturally patchy habitat type, we might expect wetland bird communities to follow island biodiversity patterns. Here we use a dataset of 2012 wetlands in Europe to explore which of a suite of environmental factors (wetland area, habitat diversity, elevation, latitude, local human population density, wetland isolation) explain species richness and diversity in wetland bird communities and whether threatened species respond in the same way to all other species. The aim of our study was to identify the most important aspects of wetlands in Europe and make management recommendations for existing wetlands and policy recommendations for conserving wetlands in the wider landscape in the context of ongoing degradation of wetlands by people.

## **METHODS**

We collected information on all Important Bird Areas (IBAs) in Europe that contain wetlands using the BirdLife International site database (Birdlife International 2006) to collate a dataset of wetland bird community structure and environmental characteristics at 2012 IBAs across Europe.

In this analysis, we considered wetland birds to be all species that are ecologically dependent on wetlands (Tucker & Evans 1997; Appendix 1). We recorded the numbers of individuals of each species in each site in 1996 and 1997. In this analysis we did not distinguish between breeding and wintering birds.

### *Response variables*

We constructed three sets of models, using three response variables: absolute species richness, number of threatened species and Shannon-Weiner diversity at each site.

### *Explanatory variables*

We recorded the area in hectares of each IBA and the proportion of the IBA which was wetland. By multiplying these variables we made a derived variable, wetland area.

Wetland area was log transformed prior to analysis.

We recorded, using dummy variables, whether the following wetland habitat types were present in the IBA: coastal lagoons; estuaries and intertidal flats; deltas; salinas; saltmarshes; standing freshwater; rivers and streams; raised bogs; fens, transition mires and springs; marshes; water fringe vegetation. By summing the number of these habitat classes we produced a habitat diversity score between one and eleven.

We recorded the latitude and longitude of each site in decimal degrees in order to use latitude as an explanatory variable, to extract spatially referenced explanatory variables from spatial datasets and in order to allow spatial autocorrelation to be incorporated in models. We also recorded the elevation of the IBA in metres above sea level.

Using zonal statistics in ArcGIS, we measured the median human population density, a *proxy* measure of the intensity of human impact on wetlands, in circles of radius 5km around each IBA using a 1km resolution gridded human population density coverage derived from census data (Dobson *et al.* 2000). Human population density was log transformed prior to analysis.

We also calculated the distance in kilometres from each site to its nearest neighbour, a *proxy* measure of isolation from other wetland habitats and connectivity. Distances were log-transformed prior to analysis.

### *Models*

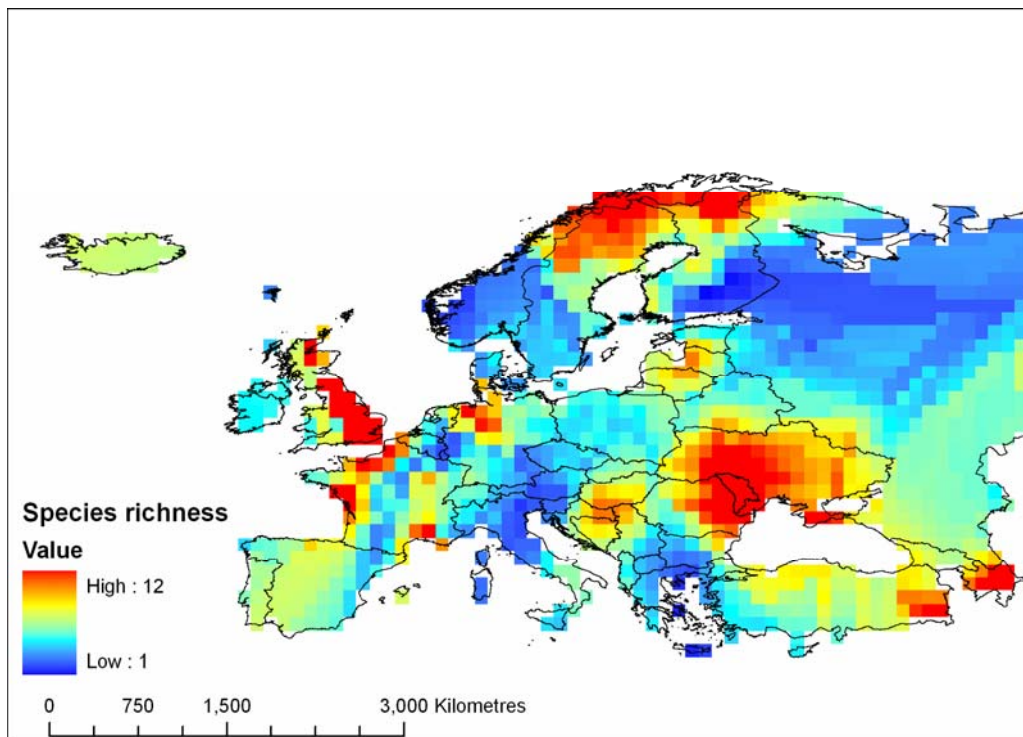
We used Generalised additive models (GAMs) to first construct bivariate models including a single explanatory variable. We then constructed minimum adequate models of species richness and diversity by first constructing a maximal model using all

individually significant variables. Secondly we removed least significant terms from a maximal model using the Akaiake Information criterion to determine when the minimum adequate model had been reached (Burnham & Anderson 2002).

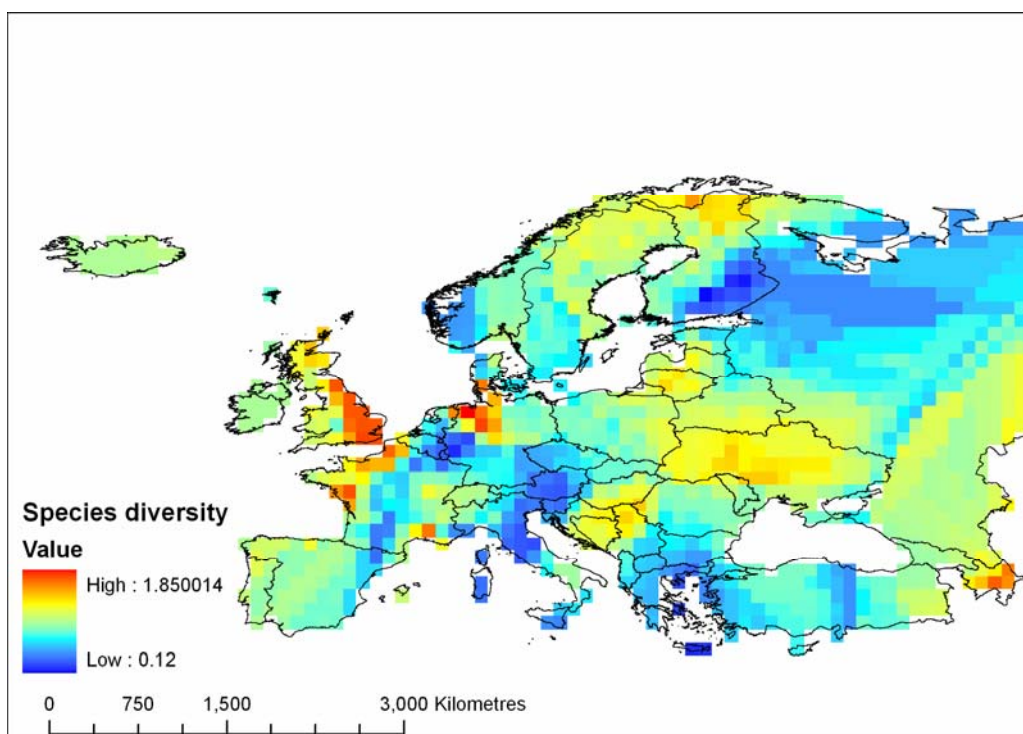
We used the R package, generalized regression and spatial prediction (GRASP; Lehman *et al.* 2002; available from <http://www.cscf.ch/grasp>) to produce three sets of models of wetland bird species richness, diversity and threatened species richness with respect to the explanatory variables. We also tested for spatial trends in the explanatory variables using linear regression. All statistical analysis was performed in R (Ihaka & Gentleman 1997). Generalised additive models (GAMs) were used instead of generalised linear models (GLMs) since a GAM can be used to fit a non-parametric smoothing function instead of fitting a parametric relationship between the response and explanatory variables. We believe this approach is most appropriate to describe complex non-linear ecological processes operating over space (Hastie & Tibshirani 1990). We also calculated an auto-covariate for each response variable using a moving window approach to allow us to account for spatial autocorrelation in our data by fitting models including our explanatory variables and an auto-covariate term (Augustin *et al.* 1996).

## **RESULTS**

European wetlands with the highest wetland bird species richness are found in Northern Scandinavia, on the Northeast coast of the UK, Northern France, the Baltic, Eastern Turkey and North of the Aral sea (Figure 1). The most diverse European wetland bird communities are in wetlands surrounding the North Sea and the Baltic sea (Figure 2).



**Figure 1:** Spatial interpolation of wetland bird species richness in Europe on a 1° grid



**Figure 2.** Spatial interpolation of wetland bird diversity in Europe on a 1° grid



Larger wetlands have greater species richness ( $r = 0.241$ ,  $p < 0.001$ ,  $n = 2012$  wetlands). Wetlands at lower elevation have greater species richness ( $r = -0.005$ ,  $p = 0.161$ ,  $n = 2012$  wetlands). Wetlands at more southern latitudes have greater species richness ( $r = -0.058$ ,  $p = 0.019$ ,  $n = 2012$  wetlands). Wetlands closer to other wetlands have greater species richness ( $r = -0.651$ ,  $p = 0.023$ ,  $n = 2012$  wetlands). Wetlands with lower local human population density have greater species richness ( $r = -0.054$ ,  $p = 0.041$ ,  $n = 2012$  wetlands). There is no association between habitat diversity and species richness ( $r = 0.452$ ,  $p = 0.232$ ,  $n = 2012$  wetlands).

**Table 1.** Species richness, number of threatened species and diversity (response variables) in relation to environmental characteristics (generalised additive model)

Response variable	Explanatory variable	r	Number of sites	p
Species richness	Wetland area	0.241	2012	<0.001
	Habitat diversity	0.452	2012	0.232
	Elevation	-0.005	2012	0.016
	Latitude	-0.058	2012	0.019
	Distance to nearest neighbour	-0.651	2012	0.023
	Human population density	-0.054	2012	0.041
Threatened species	Wetland area	0.235	2012	<0.001
	Habitat diversity	0.011	2012	0.423
	Elevation	0.024	2012	0.652
	Latitude	-0.831	2012	0.017
	Distance to nearest neighbour	-0.120	2012	0.214
	Human population density	-0.026	2012	0.038
Species diversity	Wetland area	0.134	2012	0.001
	Habitat diversity	-0.034	2012	0.598
	Elevation	-0.001	2012	0.024
	Latitude	-0.001	2012	0.825
	Distance to nearest neighbour	-0.543	2012	0.015
	Human population density	-0.031	2012	0.046

Larger wetlands have greater numbers of threatened species ( $r = 0.235$ ,  $p < 0.001$ ,  $n = 2012$  wetlands). Wetlands at more southern latitudes have greater number of threatened species ( $r = -0.831$ ,  $p = 0.017$ ,  $n = 2012$  wetlands). Wetlands with lower local human population density also have greater numbers of threatened species. ( $r = -0.026$ ,  $p = 0.038$ ,  $n = 2012$  wetlands). There was no association between habitat diversity and number of threatened species ( $r = 0.011$ ,  $p = 0.423$ ,  $n = 2012$  wetlands) or between elevation and numbers of threatened species ( $r = 0.024$ ,  $p = 0.652$ ,  $p = 2012$  wetlands) or between the distance to the nearest neighbouring wetland and threatened species ( $r = -0.120$ ,  $p = 0.214$ ,  $n = 2012$ ).

Larger wetlands have greater species diversity ( $r = 0.134$ ,  $p < 0.001$ ,  $n = 2012$  wetlands). Wetlands at lower elevation have greater species diversity ( $r = -0.001$ ,  $p = 0.024$ ,  $n = 2012$  wetlands). Wetlands closer to other wetlands have greater species diversity ( $r = -0.543$ ,  $p = 0.015$ ,  $n = 2012$  wetlands). Wetlands with lower local human population density have greater species diversity ( $r = -0.031$ ,  $p = 0.046$ ,  $n = 2012$  wetlands). There is no association between habitat diversity and species diversity ( $r = -0.034$ ,  $p = 0.598$ ,  $n = 2012$  wetlands) or between latitude and species diversity ( $r = -0.001$ ,  $p = 0.825$ ,  $n = 2012$  wetlands).

In the minimum adequate model relating to species richness, wetland area, elevation and latitude were retained in the final model (Table 2). The minimum adequate model (MAM) for the number of threatened species suggests that wetland area and latitude are the only important predictors (Table 2). The MAM for overall species diversity retained wetland area, elevation and distance to nearest neighbour (Table 2).

**Table 2.** Minimum adequate models of species richness, species diversity and threatened species richness (stepwise generalised additive model)

Response variable	Explanatory variable	B	t	p
Species richness	Wetland area	1.345	4.509	<0.001
	Elevation	-0.013	-2.629	0.009
	Latitude	-0.073	-2.436	0.017
Full model: $r^2 = 0.434$ , $F_{3,2012} = 102.31$ $p < 0.001$				
Excluded variables: Distance to nearest neighbour, Human population density				
Slope (B), t-test statistic (t) and probability of t-test statistic (p)				
Response variable	Explanatory variable	B	t	p
Species diversity	Wetland area	0.1407	3.561	<0.001
	Elevation	-0.001	-2.647	0.009
	Distance to nearest neighbour	-0.027	-2.121	0.031
Full model: $r^2 = 0.381$ , $F_{3,1448} = 61.31$ $p < 0.001$				
Excluded variables: Elevation, Human population density				
Slope (B), t-test statistic (t) and probability of t-test statistic (p)				
Response variable	Explanatory variable	B	t	p
Threatened species richness	Wetland area	0.188	3.125	<0.001
	Latitude	-0.612	-2.011	0.072
Full model: $r^2 = 0.181$ , $F_{2,2012} = 48.24$ $p < 0.001$				
Excluded variables: Human population density				
Slope (B), t-test statistic (t) and probability of t-test statistic (p)				

## DISCUSSION

In common with other studies of wetland bird communities at smaller scales (Findlay & Houlihan 1997; Guadagnin & Maltchik 2007) we found that habitat area is the most important single factor in structuring wetland bird communities. Many studies in a diverse range of taxonomic groups have demonstrated a close relationship between species richness and habitat island area (Whittaker 1998). These relationships may be due to

either a positive relationship between island area and total habitat availability or a positive relationship between habitat area and habitat diversity (Williams 1964). In this study we attempted to distinguish these closely related effects by also testing measures of habitat diversity.

Surprisingly, habitat diversity was not a significant explanatory variable in any of the models. This suggests that for wetland birds, relatively large areas of homogenous natural habitat are more important than habitat mosaics at the spatial resolution studied.

Elevation was retained in the MAMs for species richness and species diversity. These results give a useful reminder of the diversity of lowland wetlands, but it is important to remember that turnover of species also occurs along elevational gradients so is important to also conserve high elevation sites despite being associated with fewer species since some wetland bird species are restricted to upland areas.

Taken together, our results suggest that despite human modification of wetlands in Europe over hundreds of years, patterns of diversity in wetland bird communities accord with the predictions of island biogeography theory, suggesting that it is possible to generalise the patterns we see in Europe to less well studied wetland systems elsewhere in the world.

Nearest neighbour wetland distances were retained in the species diversity MAM. This is evidence to suggest that configuration of wetland habitat is important in maintaining diverse communities. This finding is relevant to the management of agricultural land and its potential to make a contribution to biodiversity conservation in the matrix between patches of habitat managed for biodiversity. Large numbers of small, perhaps temporary, wetlands may be a key factor in maintaining functional connectivity between natural wetlands and conserving the existing level of biodiversity.

It is encouraging that HPD is not retained in any of the MAMs. This may be an artefact of the scale of measurement of human impacts or a limitation of the data product used to measure human effects, but if not it suggests that high human population densities are not

incompatible with wetland biodiversity. If agricultural and recreational landscapes are managed appropriately with sensitivity to biodiversity, there should be no reason for people not to sustainably use wetlands in Europe without impacting biodiversity.

Monitoring is crucial in assessing trends in biodiversity and in evaluating the efficacy of conservation measures (Danielsen et al 2005). In this study, wetland birds species richness and diversity respond in very similar ways to environmental factors. This implies that even the simplest monitoring is worthwhile as even limited data on species richness of a site is worth knowing.

The relationships we report here allows us to identify priority wetlands in Europe in terms of biodiversity. Our findings suggest the need to conserve networks of large contiguous undisturbed areas of wetland, especially at low elevations in Southern Europe.

Unfortunately, these happen to be Europe's most threatened wetlands. Many have been lost in the recent past due to infrastructure development, tourism and agriculture.

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### **REFERENCES**

Augustin, N.H., Muggleston, M.A., Buckland, S.T. (1996) An autologistic model for the spatial distribution of wildlife. *Journal of Applied Ecology* 33: 339-347

BirdLife International (2001) *Important Bird Areas and potential Ramsar Sites in Europe*. BirdLife International, Wageningen, The Netherlands.

- Brotons L, Monkkonen M, Martin JL (2003) Are fragments islands? Landscape context and density–area relationships in boreal forest birds. *American Naturalist* 162:343–357
- Brown, M., Dinsmore, J.J. (1986) Implications of marsh size and isolation for marsh bird management. *Journal of Wildlife Management* 50:392–397
- Coleman, B.D. (1981) On random placement and species–area relations. *Mathematical Bioscience* 54:191–215
- Connor, E. F., & McCoy, E. D. (1979) The statistics and biology of the species-area relationship. *American Naturalist* 113: 789–796.
- Crooks, K.R., & Sanjayan, M. (eds.) (2006) *Connectivity conservation*. Cambridge University Press.
- Danielsen F., Burgess N., & Balmford A. (2005) Monitoring matters: examining the potential of locally-based approaches. *Biodiversity and Conservation* 14: 2507-2542
- Diamond, J.M. (1976) Island biogeography and conservation—strategy and limitations. *Science* 193:1027–1029
- Dobson, J.E., Bright, E.A., Coleman, P.R., Durfee, R.C., & Worley, B.A. (2000) Landscan: a global database for estimating populations at risk. *Photogrammetric Engineering and Remote Sensing* 66: 849-859
- Dugan, P. (1990) *Wetland conservation: a review of current issues and required action*. Gland, Switzerland. International Union for the Conservation of Nature
- Fairbairn, S.E., Dinsmore, J.J. (2001) Local and landscape-level influences on wetland bird communities of the prairie pothole region of Iowa, USA. *Wetlands* 21:41–47

Findlay, C.S., & Houlihan, J. (1997) Anthropogenic correlates of species richness in Southeastern Ontario wetlands. *Conservation Biology* 11: 1000-1009

Finlayson, M., Hollis, T., & Davis, T. (eds.) (2002) *Managing Mediterranean wetlands and their birds: proceedings of an International Waterfowl and Wetlands Research Bureau Symposium, Grado, Italy*. Slimbridge, UK: International Waterfowl and Wetlands Research Bureau (IWRB).

Guadagnin, D.L., & Maltchik, L. (2007) Habitat and landscape factors associated with Neotropical waterbird occurrence and richness in wetland fragments. *Biodiversity Conservation* 16: 1231-1244

Hastie, T., & Tibshirani, R. (1990) *Generalised additive models*. Chapman and Hall, London.

Hollis, G. E. & Jones T. A. (1991) Europe and the Mediterranean Basin. In: *Wetlands* Finlayson, M., & Moser, M. (eds) pp. 27–56. International Waterfowl and Wetlands Research Bureau, Slimbridge.

Ihaka, R., & Gentleman, R. (1996) R. A language for data analysis and graphics. *J. Comput. Graph. Stat.* 5: 299-314

Lehman, A., Overton, J., Leathwick, J.R. (2002) GRASP: Generalized regression analysis and spatial predictions. *Ecological Modelling* 157: 189-207

Lomolino MV (2000) Ecology's most general, yet protean pattern: the species–area relationship. *Journal of Biogeography* 27:17–26

MacArthur RH, Wilson EO (1967) *The theory of island biogeography*. Princeton University Press, Princeton

Moser, M., Prentice, C. and Frazier, S. (1996). A global review of wetland loss and degradation. *In*: Papers, Technical Session B, Vol 10 Proc. 6th Meeting of the Conference of Contracting Parties, Brisbane, Australia, 19–27 March 1996, Ramsar Convention bureau, Gland, Switzerland, pp. 21–31.

Riffell, S.K., Keas, B.E., Burton, T.M. (2001) Area and habitat relationships of birds in Great Lakes coastal wet meadows. *Wetlands* 21:492–507

Tucker, G.M. & Evans, M.I. (1997) *Habitats for birds in Europe: a conservation strategy for the wider environment*. Cambridge, UK. BirdLife International (BirdLife conservation series no. 6)

Whittacker, R.J. (1998) *Island biogeography: ecology, evolution and conservation*. Oxford University Press

Wiens, J.A. (1995) Habitat fragmentation - Island versus landscape perspectives on bird Conservation. *Ibis* 137:S97–S104

Williams, C.B. (1964) *Patterns in the balance of nature*. Academic Press, New York.



## **Chapter 6** Global wetland change between 1982 and 2000 as detected from AVHRR data

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### **Manuscript**

#### **Details and extent of the contributions by authors**

**P.R. Long:** analysis, manuscript writing (80%)

**B. Hughes:** suggestions to improve the study (5%)

**T. Székely:** general editing of the manuscript, suggestions to improve the study (5%)

**M.J. O'Connell:** general editing of the manuscript, suggestions to improve the study (10%)

## **Abstract**

Wetlands are a globally distributed, habitat type which support considerable biodiversity and provide many ecosystem services including flood defence, drinking water, fish stocks and water for agriculture. Unfortunately, wetlands are threatened by human activities and many wetlands have been lost or degraded in the past. In order to inform future national and regional priorities and action plans for wetlands, it is important to understand the geographical patterns and temporal trajectories of historical wetland changes. To address these questions we performed a change analysis of multi-temporal satellite images. We developed spectral signatures using Advanced Very high Resolution Radiometer (AVHRR) data acquired in 2000 by sampling areas identified as 100% wetland and 0% wetland at the spatial scale of our images from a global wetland inventory in order to identify the typical spectral signatures of wet areas and non-wetland areas. We then performed a soft classification of 8km resolution global AVHRR 10 day composites using linear spectral mixture analysis to estimate proportional coverage of wetlands in each month in 1982, 1985, 1988, 1991, 1994, 1997 and 2000. By calculating the minimum and maximum wetland extent in every 8km pixel in each of these years, we distinguished seasonal variation from long-term trends in wetland area over 18 years. The total area of wetlands in 2000 was 6,212,673km<sup>2</sup>. Globally, we estimate that there was a net loss of 474,278 km<sup>2</sup> of wetlands in the period 1982-2000, a 7% decrease. The trajectory of wetland loss differed between continents; in Asia 13% of wetlands were lost whereas in Europe only 2%.

## INTRODUCTION

Wetlands are a globally distributed habitat type which includes lakes, rivers, marshes, bogs, fens, mangroves, saltmarshes and flooded forests. Wetlands support considerable biodiversity and due to their high productivity and hydrology, provide many ecosystem services and functions to people such as provision of fresh water for drinking and agriculture, fisheries, flood defence, pollution dilution, transport infrastructure, and recreational uses. Inventories of the global extent of wetlands have very provided valuable baseline information about this habitat (Finlayson & Davidson 1999; Matthews & Fung 1987; Lehner & Doll 2004). Unfortunately, wetlands are also considerably threatened by human activities and many wetlands have been lost or degraded in the past. In order to inform wise future management of wetlands, it is important to understand the geographical patterns and temporal trajectories of historical wetland changes. The magnitude of wetland change over several time periods have been estimated in some regions of the world (Dahl 1990; National Wetlands Working Group 1988; Lu 1995; Revenga et al 2000). However there has been no comparable study of the global pattern of wetland change.

Remote sensing is a powerful tool to map wetlands and also to explore wetland change at small spatial scales (<10km) and over large spatial extents (reviewed by Ozesmi & Bauer 2002). The limitation of most wetland inventories is that they are snapshots at a given time and it is usually not possible to compare wetland inventories conducted at different times to estimate wetland change due to varying methods between inventories. To address these issues we performed a global change analysis using multi-temporal satellite images.

In this study, we use a time series of data from the Advanced Very High Resolution Radiometer (AVHRR) sensor to explore global patterns of wetland change over an 18 year period. The AVHRR is a sensor which has been mounted on a number of polar-orbiting environmental satellites (POES) operated by the National Oceanic and Atmospheric Administration (NOAA) since 1979. The first AVHRR sensor was carried on TIROS-N.

The AVHRR/2 sensor, augmented with a fifth band, was carried by NOAA-7 in 1981. The latest version of the sensor, AVHRR/3, was first launched aboard NOAA-15 in 1998 and has subsequently been fitted to NOAA-16, NOAA-17 and NOAA-18. The AVHRR/3 instrument is able to image a sixth, mid-infrared, band in addition to the bands common to the original AVHRR and AVHRR/2 sensors (Lillesand et al 2008).

The AVHRR sensors were designed to collect meteorological data. However, since the satellites carrying AVHRR sensors provide global coverage with a daily repeat cycle, and consistently calibrated data have been collected and archived over long time periods, AVHRR data have proved very useful for environmental studies of phenomena at continental and global scales for which the relatively coarse spatial grain of AVHRR data is acceptable (Los et al. 2000).

Although AVHRR data are a powerful data source to address many global questions there are several limitations which must be overcome. First, the AVHRR/3 sensor collects 15Gb of data every day. The enormous data volume of the AVHRR archive is a major obstacle to its effective use. Second, an individual orbital segment of raw AVHRR data contains considerable noise and is very likely to include substantial cloud cover. Considerably more post-processing of AVHRR data is necessary before they can be used to study land cover than is needed to observe the meteorological phenomena the satellites were designed to monitor.

To classify coarse-scale remote sensed data which inevitably contains cells which contain a mixture of land cover types known as 'mixed pixels', a number of soft-classification techniques have been developed which differ from traditional hard-classification procedure which attempt to unambiguously allocate cells to a limited number of pre-determined cover types based on spectral similarity to training data. Linear spectral mixture methods assume that the reflectance of a pixel in each band it is imaged in is a linear combination of the contributions of the reflectances of each land cover type present in the mixed pixel in proportion to the area of that cover type (Settle & Drake 1993). If

the spectral characteristics of the components of the land cover mixture are known, is then possible to infer the proportion contribution of each to the observed spectral mixture. Spectral unmixing procedures have proved useful in estimating proportional coverage of agricultural crops (Quamby et al 1992), and vegetation proportion (Defries et al 2000). Mixture models also typically outperform hard classifiers with coarse-scale data (Cross et al 1991), mostly because as the spatial grain of remote sensed data gets larger, it becomes increasingly likely that pixels will contain a mixture of land cover types and because the probability of misplacement in a category bin also increases. A critical step in linear spectral unmixing is making appropriate spectral signatures for the most pure examples of the land cover types which are present. These spectral signatures are known as 'endmembers'. This is accomplished by finding areas of the landscape which are pure examples (100% coverage) of the target landcover at the spatial scale of the imagery to be classified.

## **METHODS**

We chose to use three bands of AVHRR data: band 1 is visible red light 0.58-0.68 $\mu$ m, band 2 is near infra-red radiation 0.73-1.00 $\mu$ m and band 4 is broad spectrum thermal radiation 10.30-11.30 $\mu$ m.

### *Image processing*

We used a set of 10 day AVHRR composites for every 10 day period from 1982-2000 that were produced by the Pathfinder 8km project (Agbu & James 1994). Although this data product has not been produced since 2001 and is no-longer archived by Goddard Earth Science Distributed Active Archive Center (GES DAAC), it is available from the International Water Management Institute (IWMI), Sri Lanka [available from url: <http://www.iwmidsp.org/iwmi/info/main.asp>].

During processing of each 10 day Pathfinder global land composite, many orbital passes were stitched together, and corrections were made to the imagery to account for

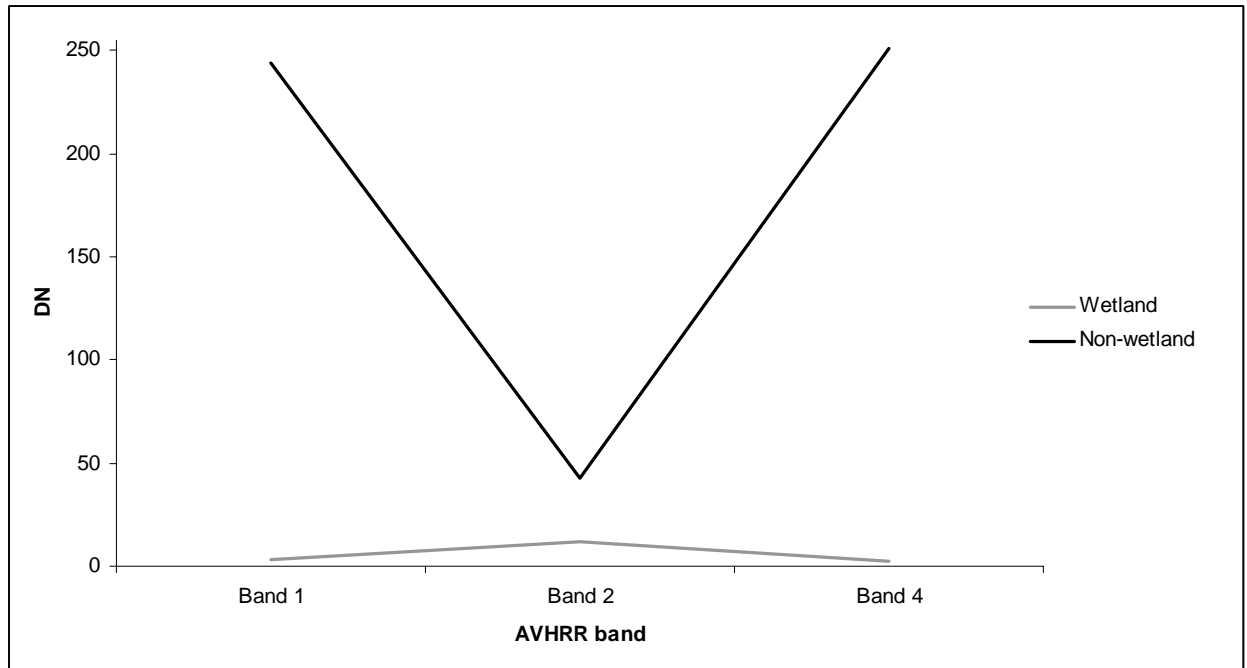
atmospheric attenuation and atmospheric radiance (Holben 1986). Due to sensor failure there is a three month gap from October-December 1994.

In this study, all image processing was performed using Idrisi Kilimanjaro (Eastman 2003). We imported all 10 day composites for all bands and windowed each image to remove Antarctica and the region south of 60° South. We then made monthly maximum composites from each set of three 10 day composite images for each month for each band separately. This further lessened the effects of clouds, eliminated noise, discarded dropped pixels and had the effect of selecting the pixels from the nearest to the satellites' nadir view.

#### *Development of endmember signatures and validation data*

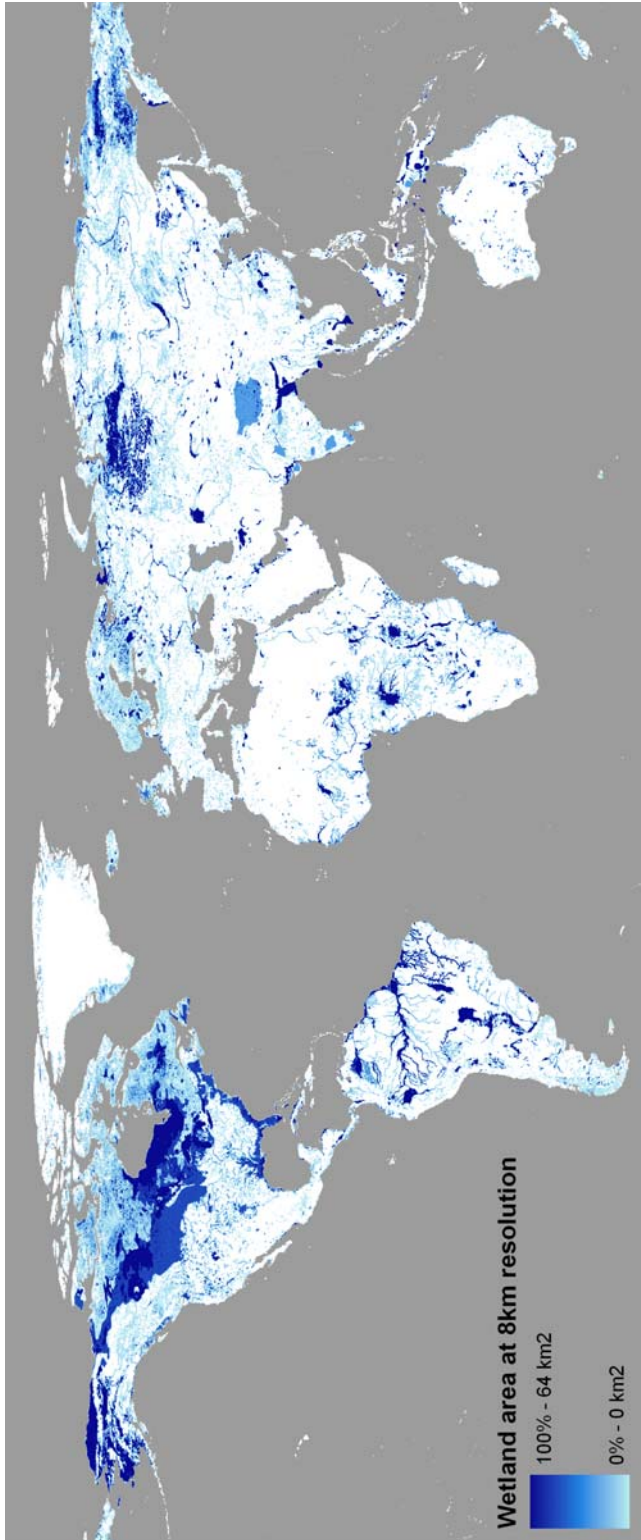
First, we developed a single collection of bands from which to make signatures by taking reflectance data from all months in the year 2000 and composing these into a single annual mean value for each band. Second, we derived a layer of 'ground-truth' independent of the remote sensed AVHRR data. In order to do this we used the GLWD3 grid in the global lakes and wetland database (Lehner & Doll 2004), [available from url: <http://www.worldwildlife.org/science/data/item1877.html>] to find the proportional wetland area at 8km resolution according to this wetland inventory. Then we extracted the proportional area of wetland in the 8km to a field in a point coverage at the same spatial resolution. It was then necessary to rarify this set of points such that there were an equal number in each 10 degree latitude band in order that the spectral characteristics of wetlands in latitudes which have proportionally more land (such as northern Canada and Siberia) do not overdominate the wetland endmember. Next, we selected only those points which corresponded with 0.1 degree cells which contained either 100% wetland or 0% wetland according to the GLWD3 inventory. These two sets of points were then randomly partitioned into equal-sized training and validation sets. The set of training points were then converted to two multipart polygon shapefiles composed of 8km cells centred on the points – one shapefile containing a global sample of 100% wetland cells and another containing a global sample of 0% wetland cells. Finally, we

used the two training polygons and the year 2000 composites to make spectral signatures in three AVHRR bands for the 100% wetland and 0% wetland endmembers in the year 2000.



**Figure 1.** Spectral signatures of endmembers used to define non-wetland and wetland. AVHRR Band 1 is visible red light 0.58-0.68 $\mu$ m. Band 2 is near infra-red radiation 0.73-1.00 $\mu$ m. Band 4 is broad spectrum thermal radiation 10.30-11.30 $\mu$ m.

Since the classification procedure unmixes the spectra of each 8km cell to estimate wetland proportion from 0-100%, it is necessary to validate the sub-pixel classification across this full range. Thus, in contrast to hard classifiers, a validation data set can not be made by simply partitioning the data used to develop signatures. Instead, we made a validation dataset by taking the set of points corresponding to 0% wetland and 100% wetland cells reserved for validation during signature development and combining these with a random selection of half of all the other points corresponding to cells containing between 1% and 99% wetland which remained after rarifying the original point coverage by latitude.



**Figure 2.** Global wetland area at 8km resolution in 2000.



### *Classification*

We performed sub-pixel classification of band collections for all months in 1982, 1985, 1988, 1991, 1994, 1997 and 2000 (with the exception of October, November and December in 1994) and also of the year 2000 annual composite using the linear spectral unmixing procedure implemented in Idrisi Kilimanjaro (Settle & Drake 1993; Shimabukuro & Smith 1991).

### *Validation*

To validate the accuracy of our classifier we considered only the classification of the year 2000 annual composite, since no independent data concerning wetland distribution seasonally were available. We used the 10000 8km cells to calculate a Kappa coefficient  $((\text{Observed agreement} - \text{Chance agreement}) / (1 - \text{Chance agreement}))$  of agreement of a cross-tabulation (contingency table) containing the frequency of each contingency of twenty 5% ranges of proportional wetland area as classified by our linear mixture model compared to the independent Lehner & Doll (2004) dataset.

### *Seasonality*

Having estimated the proportional wetland coverage of each 8km cell in all months in seven years, it was necessary to quantify the seasonal variation in wetland extent each year. To do this we used map algebra to make a map for each year in which each cell took as its value the minimum wetland proportion in that year. We repeated this method to also find the maximum wetland proportional area of each cell in each of our seven study years. This approach allowed wetland extents from different months to be selected in different parts of the world. We reasoned that the annual wetland extent of a given pixel must lie between the annual minimum and maximum, and estimated this by taking a midpoint. By considering seasonal effects in this way we reduced data volume from 81 classified maps to 21 maps (7 annual minimums, 7 annual maximums, 7 annual midpoints).

### *Change analysis*

We took a histogram of each of the maps produced by the seasonality process to find the cumulative frequency of cells containing some proportion of wetland. Multiplication of each wetland proportional area by the  $64\text{km}^2$  (the area of an 8km cell) allowed us to estimate global wetland area in each year. We also disaggregated our results by continents by masking prior to extracting histograms from the classified maps. We produced a global map net wetland change in the period 1982-2000 by subtraction of the 2000 midpoint wetland extent map from the 1982 midpoint wetland extent map.

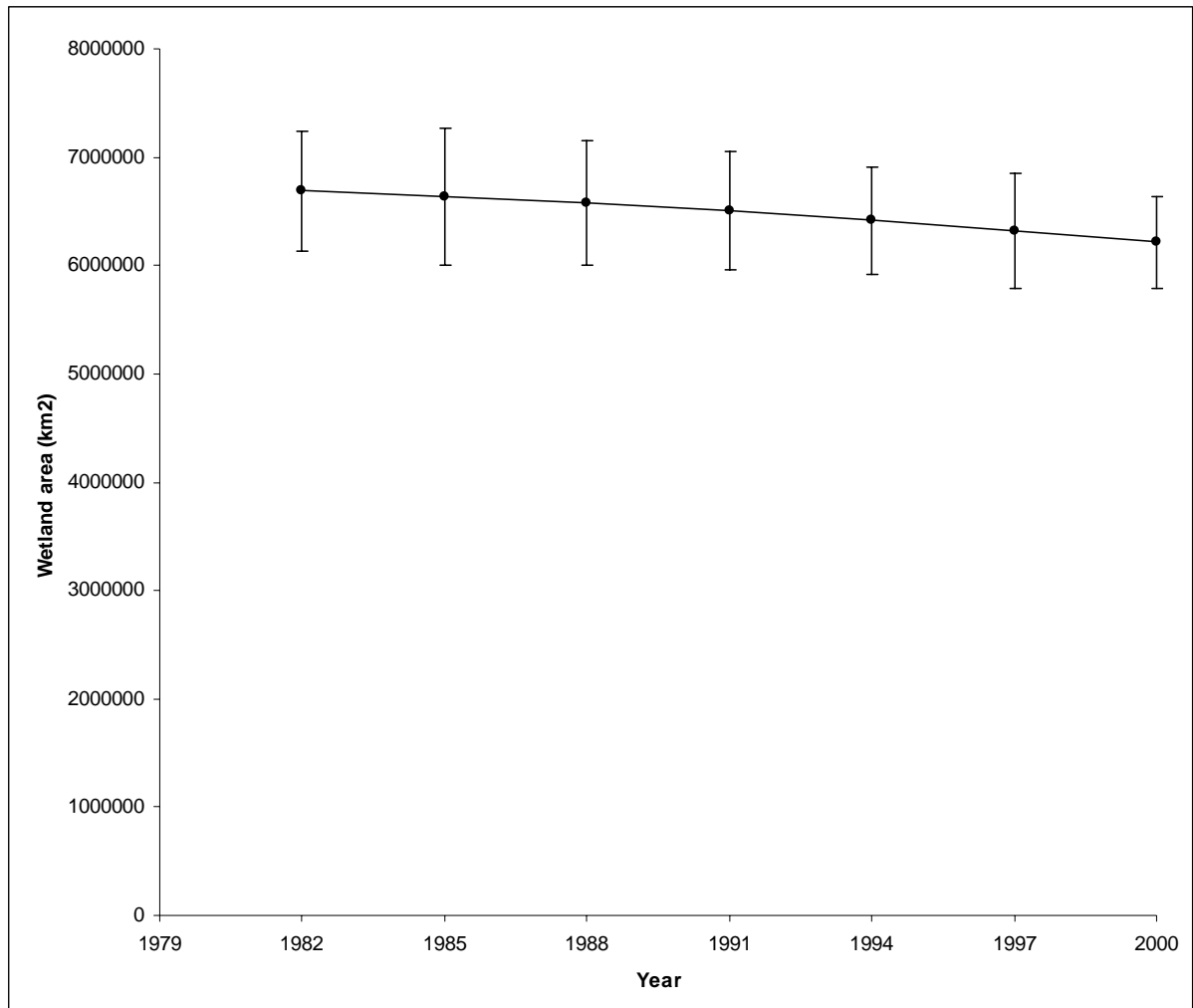
## **RESULTS**

Wetlands have a substantially different absorption spectrum from non-wetland in the AVHRR band that we studied, which allowed the creation of distinct endmembers (Figure 1). Linear spectral unmixing of a year 2000 AVHRR data produced a classified map of proportional wetland area (Figure 2) which allowed us to validate our classifier. The Kappa coefficient of agreement of our soft-classifier ( $\kappa$ ) was 0.94, indicating exceptionally high classification accuracy.

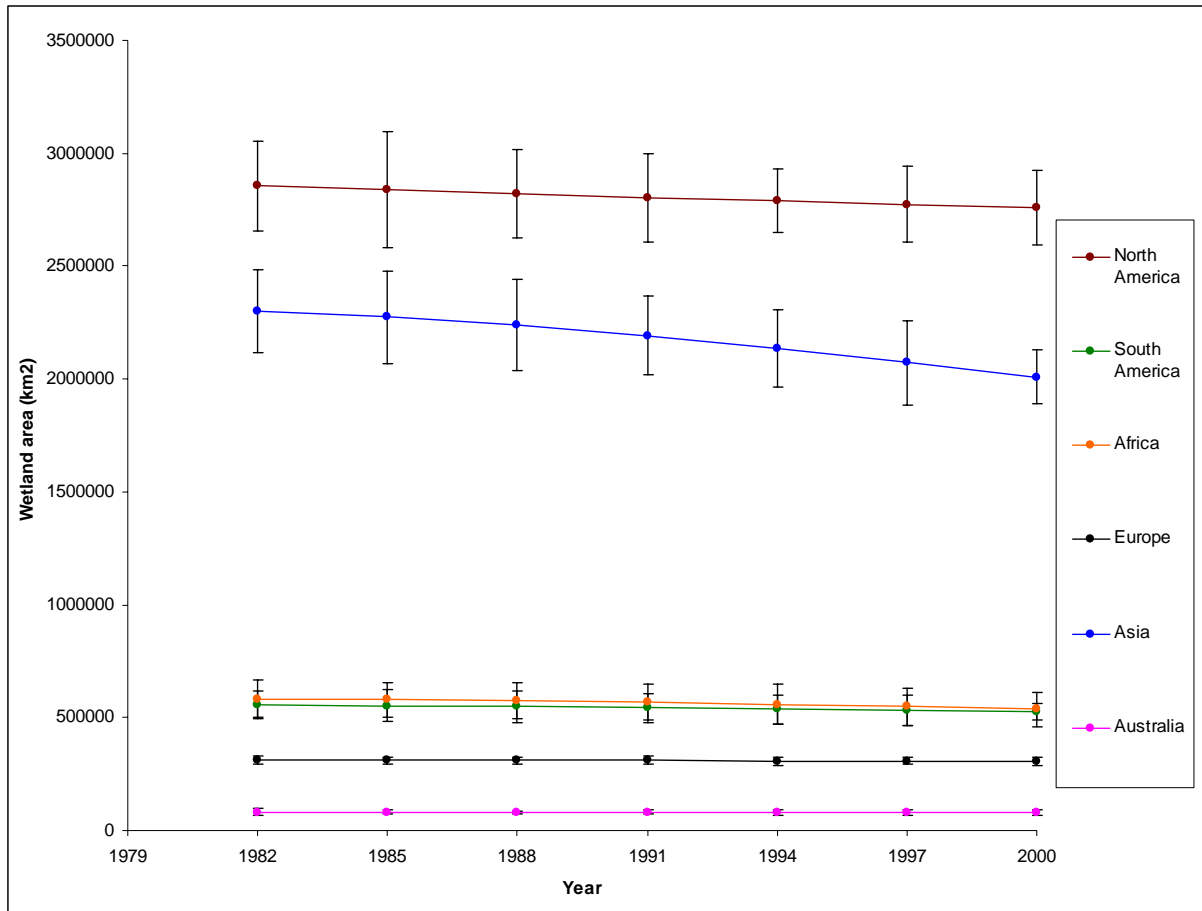
Seasonal variation in wetland extent was considerable, but it was nonetheless possible to see clear trends in wetland area over the 18 year period studied. Globally there was a net loss of  $474,277\text{ km}^2$  (7.51%) of wetland area between 1982 and 2000 (Table 1, Figure 3). The rate of change was not consistent between continents; In Europe 1.96% of wetlands were lost in this period, whereas in Asia 15.01% of wetlands were lost (Table 1, Figure 4). Wetland changes occurred by conversion of cells which contained some wetland to non-wetland and by changes in the proportional area of wetlands in some cells (wetland degradation and fragmentation). Relatively few 8km cells (0.04%) experienced a net increase in wetland area in the 18 year period studied. The geographical pattern of wetland change was far from uniform. The Arctic and tropical rivers in particular have lost considerable wetland area in the recent past (Figure 5).

**Table 1.** Wetland area estimates (km<sup>2</sup>) for the period 1982-2000 disaggregated by continent.

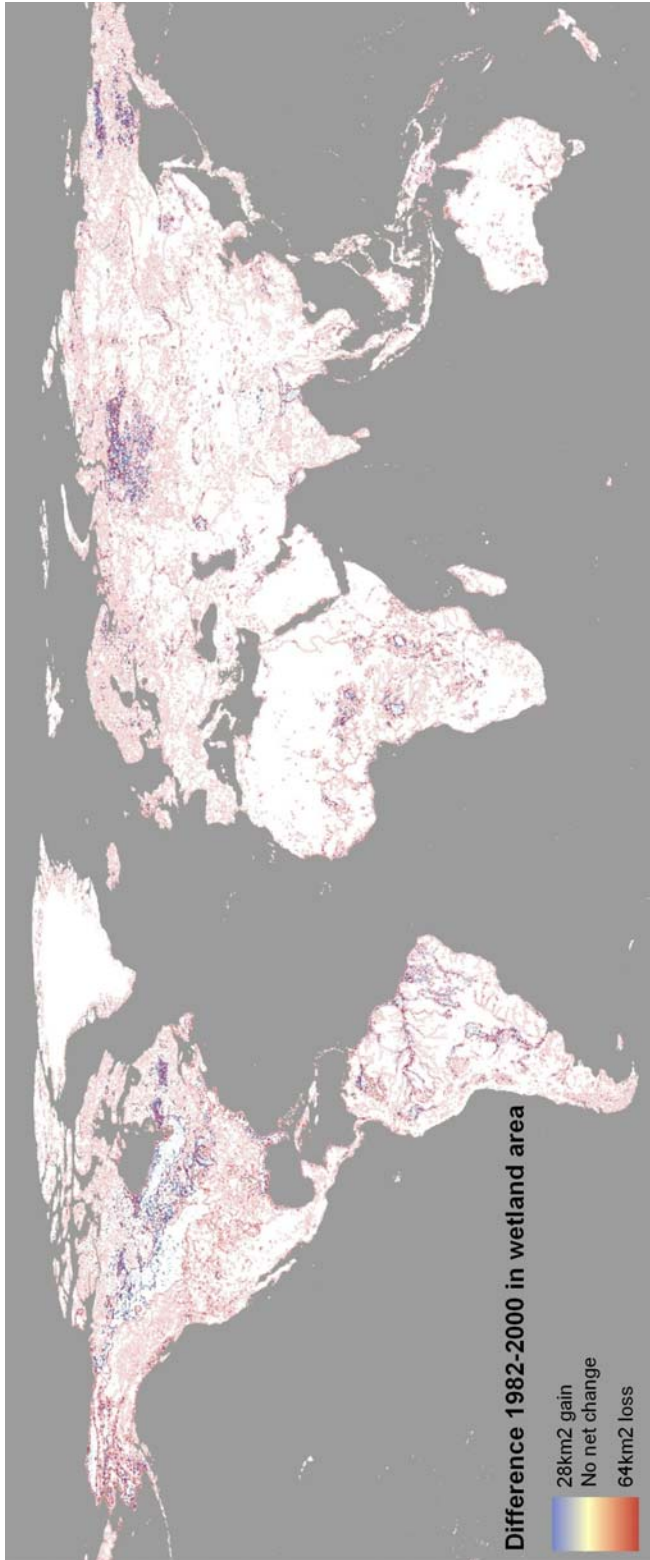
Region	Estimate	Year							Percentage wetland loss between 1982 and 2000
		1982	1985	1988	1991	1994	1997	2000	
North America	Minimum extent	2654957	2583220	2622786	2608321	2651422	2608387	2592759	3.38%
	Midpoint	<b>2854793</b>	<b>2838703</b>	<b>2820200</b>	<b>2804646</b>	<b>2790970</b>	<b>2774880</b>	<b>2758254</b>	
	Maximum extent	3054628	3094186	3017614	3000972	2930519	2941373	2923749	
South America	Minimum extent	495524	481482	477554	478355	473509	462629	487565	5.84%
	Midpoint	<b>556768</b>	<b>553427</b>	<b>548913</b>	<b>543586</b>	<b>538078</b>	<b>531758</b>	<b>524264</b>	
	Maximum extent	618013	625373	620271	608816	602647	600886	560962	
Africa	Minimum extent	501422	503834	494437	489931	469735	465528	460866	8.09%
	Midpoint	<b>583049</b>	<b>579119</b>	<b>574927</b>	<b>569687</b>	<b>559208</b>	<b>547680</b>	<b>535891</b>	
	Maximum extent	664676	654405	655417	649444	648681	629832	610915	
Europe	Minimum extent	293828	296146	295240	292193	292255	292264	288067	1.96%
	Midpoint	<b>312583</b>	<b>311732</b>	<b>310779</b>	<b>310779</b>	<b>310779</b>	<b>307646</b>	<b>306454</b>	
	Maximum extent	331338	327319	326318	329364	329303	323028	324842	
Asia	Minimum extent	1743155	1698240	1668261	1646318	1594573	1515445	1517212	15.01%
	Midpoint	<b>1926995</b>	<b>1902890</b>	<b>1869947</b>	<b>1821737</b>	<b>1765493</b>	<b>1702017</b>	<b>1637737</b>	
	Maximum extent	2110834	2107540	2071632	1997156	1936412	1888588	1758261	
Australasia	Minimum extent	68680	71622	73656	70761	66307	68383	66422	3.29%
	Midpoint	<b>81762</b>	<b>81389</b>	<b>80941</b>	<b>80411</b>	<b>79888</b>	<b>79515</b>	<b>79074</b>	
	Maximum extent	94844	91156	88226	90060	93469	90647	91726	
World	Minimum extent	5757566	5634544	5631934	5585879	5547801	5412636	5412891	7.51%
	Midpoint	<b>6315950</b>	<b>6267262</b>	<b>6205706</b>	<b>6130846</b>	<b>6044416</b>	<b>5943495</b>	<b>5841673</b>	
	Maximum extent	6874333	6899979	6779478	6675812	6541031	6474354	6270455	



**Figure 3.** Global trajectory of net change in wetland area 1982-2000. Vertical bars show seasonal maximum and minimum wetland extents.



**Figure 4.** Trajectories of net change in wetland area 1982-2000 by continent. Vertical bars show seasonal maximum and minimum wetland extents.



**Figure 5.** Global distribution of net wetland change 1982-2000 at 8km resolution

## DISCUSSION

This study has allowed us to robustly estimate the magnitude of net global change in wetlands over a moderately long time period and explore global patterns of wetland change and identify hotspots of wetland loss. The classifier performed extremely well when validated. This is crucial for our ability to distinguish small changes over time from classification errors.

We recognise a number of limitations in this analysis, but believe that the general patterns are nonetheless very informative. First, 8km cells are relatively large, but mixture models can nonetheless reveal interesting patterns at this spatial scale (Defries et al. 2000). Second, given that it is impossible to conduct global scale ground-truthing, we have had to assume that an independent dataset (inventory) represents wetland habitats. and then used robust signature development and validation methods ( $\kappa$  statistic) in the hope that the resultant propagated errors do not mask the trend that we want to discern. In this respect the exceptionally good calibration of the AVHRR instruments is very valuable: we may reasonably expect classification error to be more systematic than random, and thus not substantially affect any temporal trends.

It is important to note that degradation to wetlands can take forms other than land-cover change, such as pollution and invasive species which can't be observed by satellites. In this sense, wetland change analysis based on remote sensing is conservative: changes in reflectance measured by satellites will tend to underestimate the total impacts on biodiversity and ecological processes of any detected land cover changes.

In the context of climate change and human population growth, future pressures on wetlands are likely to increase. Much wetland change ultimately results from an enlarged human footprint driving greater levels of water abstraction, demands for agricultural land, more intensive freshwater fisheries, pollution and more species invasions (Postel 2003).

There are a number of ways in which this study could be extended to allow a more detailed understanding of wetland change from the AVHRR archive. First, it would be very useful to extend the time series of 8km 10 day AVHRR composites from 2000 to the present by processing recent archived AVHRR data. This would allow the most recent wetland changes to be detected and provide a standardised mechanism for future wetland monitoring which is comparable with a historical time series. Second, global 10 day AVHRR composites were produced at 1km resolution in the period 1992-1996 (Teillet et al. 2000). Applying our linear spectral unmixing methods with the same endmembers to this dataset would allow estimates of wetland proportion at a finer spatial scale, albeit for a small subset of years. Such an approach could suggest the most appropriate spatial scale at which to detect wetland changes. Third, although soft-classifiers are very useful for estimating changes, a drawback is that it is not possible to identify the exact land cover transitions by which changes have occurred. Hard classifiers which can identify the land cover types which are replacing wetlands could be used to complement linear spectral unmixing approach. Fourth, our record of the trajectory of wetland change across space should allow modelling of the probability of a change greater than a threshold magnitude as a function of landscape variables which could be associated with drivers of wetland change such as human population density, elevation and distance from the coast. Such models may allow scenarios of future wetland change to be explored, in the context of projected patterns of human growth and climate change.

Taken together, our results lead us toward a better understanding of the patterns and process of global wetland change in the recent past. Given the complexity, scale and dynamic nature of global freshwater ecosystems, further studies are needed to explore wetland changes in considerably more detail, in order to make informed contributions to environmental policy. Regional studies making use of time series of satellite images with finer spatial grain and more bands will be especially valuable in understanding changes in particular wetland types and changes at smaller spatial scales than the coarse global analysis presented here.



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## **REFERENCES**

Agbu, P.A., & James, M.E. (1994) *The NOAA/NASA Pathfinder AVHRR land data set user's manual*. Goddard Distributed Archive Center, Goddard Space Flight Center.

Cross, A.M., Settle, J.M., Drake, N.A., Paivinen, R.T.M. (1991) Sub-pixel measurement of tropical forest cover using AVHRR data. *International Journal of Remote Sensing* 12, 1119-1129

Dahl, T.E. (1990) *Wetland losses in the United States, 1780s to 1980s*. US Department of the Interior, Fish and Wildlife Service, Washington.

Daniels, A.E., & Cumming, G.S. (2008) Conversion or conservation? Understanding wetland change in Northwest Costa Rica. *Ecological Applications* 18: 49-63

Defries, R.S., Hansen, M.C., & Townshend, J.R.G. (2000) Global continuous fields of vegetation characteristics: a linear mixture model applied to multi-year 8km AVHRR data. *International Journal of Remote Sensing* 21: 1389-1414

Eastman, J.R. (2003). *Idrisi Kilimanjaro. Guide to GIS and image processing*. Worcester, MA, USA: Clark Labs.

Finlayson, M., & Davidson, N.C. (1999) *Global review of wetland resources and priorities for wetland inventory*. Ramsar Bureau Contract 56, Ramsar Conservation Bureau, Gland, Switzerland

- Frey, K.E. & Smith, L.C. (2007) How well do we know northern land-cover? Comparison of four global vegetation and wetland products with a new ground-truth database for West Siberia. *Global Biogeochemical Cycles* 21: 1016-1031
- Holben, B.N. (1986) Characteristics of maximum-value composite images from temporal AVHRR data. *International Journal of Remote Sensing* 7: 1417-1434
- Gibbs, J.P. (2000) Wetland loss and biodiversity conservation. *Conservation Biology* 14: 314-317
- Junk, W. (2002) Long-term environmental trends and the future of tropical wetlands. *Environmental Conservation* 29: 414-435
- Lehner, B., & Doll, P. (2004). Development and validation of a global database of lakes, reservoirs and wetlands. *Journal of Hydrology* 296: 1-22
- Lillesand, T.M., Kiefer, R.W., & Chipman, J. W. (2008) *Remote sensing and image interpretation. 6th edition.* Wiley.
- Los, S.O., Collatz, G.J., Sellers, P.J., Malmstrom, C.M., Pollack, N.H., DeFries, R.S., Bounoua, L., Parris, M.T., Tucker, C.J., & Dazlich, D.A. (2000) A global 9-year biophysical land surface dataset from NOAA AVHRR data. *Journal of Hydrometeorology* 1: 183-199.
- Lu, J. (1995) Ecological significance and classification of Chinese wetlands. *Vegetatio* 118: 49-56

Lu, D., & Weng, Q. (2006) Spectral mixture analysis of ASTER images for examining the relationship between thermal features and biophysical descriptors in Indianapolis, Indiana, USA. *Remote Sensing of Environment* 104: 157-167

Matthews, E., & Fung, I (1987) Methane emissions from natural wetlands: global distribution, area and environmental characteristics of sources. *Global Biogeochemical Cycles* 1: 61-86

McCarthy, J.M., Gumbrecht, T., McCarthy, T., Frost, P., Wessels, K., & Seidel, F. (2003) Flooding patterns of the Okavango wetland in Botswana between 1972 and 2000. *AMBIO: A journal of the human environment* 32: 453-457

Mitsch, W.J., & Gosselink, J.G. (2007) *Wetlands*. 4th Edn. Wiley

Monserud, R.A. & Leemans, R. (1992). Comparing global vegetation maps with the Kappa statistic. *Ecological Modelling* 62: 275–293.

National Wetlands Working Group (1988) *Wetlands of Canada*. Ecological and Classification Series 24, Environment Canada, Ottawa, Canada.

Ozesmi, S.L., & Bauer, M.E. (2002) Satellite remote sensing of wetlands. *Wetlands Ecology and Management*. 10: 381-402

Quamby, N.A., Townshend, J.R.G., Settle, J.J., White, K.H., Milnes, M., Hindle, T.L., & Stileos, N. (1992) Linear mixture modelling applied to AVHRR data for crop area estimation. *International Journal of Remote Sensing* 13: 415-425

Revenge, C., Brunner, J., Henninger, N., Kassem, K., & Payne, R. (2000) *Pilot analysis of global ecosystems: freshwater systems*. World Resources Institute. Washington.

Settle, J.J., & Drake, N.A. (1993) Linear mixing and the estimation of ground proportions. *International Journal of Remote Sensing* 14: 1159-1177.

Shimabukuro Y.E. & Smith, J.A. (1991) The least-squares mixing models to generate fraction images derived from remote sensing multispectral data. *IEEE Transactions on Geoscience and Remote Sensing* 29: 16-20.

Teillet, P.M., El Saleous, N., Hansen, M.C., Eidenshink, J.C., Justice, C.O., & Townshend, J.R.G. (2000) An evaluation of the global 1km AVHRR land dataset. *International Journal of Remote Sensing* 21: 1987-2021

Zhu, H. (2005) Linear spectral unmixing assisted by probability guided and minimum residual exhaustive search for sub-pixel classification. *International Journal of Remote Sensing* 26: 5585-5601

## Conclusion

In this thesis, I have attempted to address the wetland conservation issues across a wide range of levels of biological organisation, spatial and temporal scales. We began with a species distribution model of individuals of Madagascar plover, and then considered wildfowl populations globally, then all wetland bird species globally, and then wetland bird communities in Europe, and finally global change in wetland ecosystems.

Although the conceptual lens has become wider with each succeeding chapter, the focus throughout has remained wetland conservation. In drawing together these five studies, it is hoped that the linkages and synergies between them offer some prospects for future research. In particular, there is great scope for data derived at one spatial scale, such as characteristics of birds' global ranges being used to inform studies of processes nested inside these ranges at smaller spatial scales.

Taken together, these studies consistently suggest that wetlands face a very uncertain future. Although some species and groups are more resilient than others and some parts of the world have experienced relatively low rates of wetland loss, there are many places where wetlands are highly threatened. Effective conservation in future will rely upon evidence for the value of wetlands and plausible scenarios of the persistence of wetland ecosystems and biodiversity being marshaled and communicated to the public and key decision makers.

Many scientists, politicians and the media focus on the importance of climate change as a major threat to biodiversity and ecosystem services. However, accelerating land-use change may yet prove to be an even bigger challenge, especially for wetlands. This is why it has never been so important to monitor wetland biodiversity in key sites and develop new remote-sensing techniques to monitor wetlands synoptically over large regions.

Monitoring techniques for forest landscapes are now in a very mature state, however wetlands are very complex environments and pose huge challenges to monitoring: wetlands vary in scale from springs on the order of metres, to the great lake systems which cover hundreds of thousands of square kilometres – unlike forests, many of the world's wetlands, which support biodiversity and confer ecosystem services, are very small. Wetlands are also dynamic systems, water levels can rise and fall dramatically causing huge changes in the extent of the system. Wetlands also comprise a diverse set of land cover types including open water, trees (mangroves, flooded forests), saltmarshes, marshes and intermittently flooded grasslands.

Wetland birds are relatively well monitored, at least in Europe, but in many parts of the world, flowering plants, fish and amphibians of wetlands are poorly studied. Everywhere we are only beginning to scratch the surface of the diversity of invertebrates found in wetlands. Clearly, we need much better knowledge of wetland biodiversity to meet the challenges ahead.